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Effects of ghost fishing on the population of red king crab (*Paralithodes camtschaticus*) in Womens Bay, Kodiak Island, Alaska

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Abstract—Ghost fishing, the capture and killing of marine organisms by lost or abandoned fishing gear, is a serious ecological and economic problem confronting fisheries. In this study, we quantify the rate of ghost fishing on the population of red king crab (*Paralithodes camtschaticus*) in Womens Bay, Kodiak Island, Alaska. From 1991 to 2008, crabs with carapace lengths (CLs) from 42 to 162 mm were tagged with acoustic tags and tracked both from a boat at the surface and by divers. Diver observations were used to determine whether a crab molted or died and, in many cases, to determine the cause of death. Of 192 crabs tracked during this study in association with other projects, 13 were killed in ghostfishing gear (12 in ghost crab pots and 1 in a ghost gill net) and 20 were captured in ghost pots and released alive by divers. An additional 13 died of other causes, including predation by sea otters and an octopus and poaching by humans. We estimate that between 16% and 37% of the population of red king crab with CLs >60 mm in Womens Bay were killed by ghost fishing per year during the period of this study, making ghost fishing a substantial source of mortality. These results indicate that steps to reduce ghost fishing in Womens Bay are warranted.

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Ghost fishing is the capturing and killing of marine organisms by fishing gear that has been lost or abandoned (Smolowitz, 1978) and is a serious economic and ecological problem in fisheries around the world (Breen, 1990; Laist, 1996; Matsuoka et al., 2005). Even after they are lost, nets can continue to entangle and kill organisms (Kaiser et al., 1996; Santos et al., 2003; Baeta et al., 2009), and fish traps and crustacean pots can continue to attract, trap, and kill target and nontarget species (Stevens et al., 2000; Hebert et al., 2001; Erzini et al., 2008; Ramirez-Rodriguez and Arreguin-Sanchez, 2008), such as reptiles, birds, and mammals (Havens et al., 2008; Good et al., 2009; 2010). Dead animals in crab pots and fish nets can then act as bait to attract even more organisms (Havens et al., 2008). Although in some cases these effects are negligible, in many cases, depending on the type of gear and the environment (Gerrodette et al., 1990; Santos et al., 2003), ghost fishing represents a substantial economic loss to the fishery (e.g., Breen, 1987).

One of the major difficulties in the estimation of the effects of ghost fishing is the methods that are typically used. Many studies either recover lost gear and determine the number of organisms caught (e.g., Stevens et al., 2000) or deliberately "lose" and follow the gear over time (Bullimore et al., 2001). In both cases, however, extrapolation of the results to the population level with any certainty is difficult because of the many important factors that must be estimated on the basis of limited information, including the rate of gear loss, rate of gear decay, and population size of the study organism. In addition, animals that escape may suffer delayed mortality in response to starvation during the captivity period (Paul et al., 1994), and this effect often is unaccounted for (e.g., Breen, 1987).

In this study, we took the unique approach of tracking individuals in a population of red king crab (*Paralithodes camtschaticus*) over time and observed their fates by tagging them with acoustic tags and by making in situ observations during scuba diving. This work allowed us to calculate the mortality rate caused by ghost fishing at the population level independent of population size (e.g., Lambert et al., 2006) and to compare it directly with other causes of mortality, such as predation. In addition, rather than focusing on one particular type of gear, this approach included all types of ghostfishing gear that were catching red king crabs in the study area and allowed comparisons among these gear.

This study took place in Womens Bay, which is located in the Gulf of Alaska near the city of Kodiak on Kodiak Island, Alaska, and is a popular site for commercial, sport, and subsistence fishing for a variety of finfish and shellfish species (Fig. 1). Red king crab was the major fishery species in the Gulf of Alaska during the 1960s, but populations of this crab crashed in the 1970s and 80s. The commercial fishery was closed in 1983 and has not been reopened (Orensanz et al., 1998). Since that time, red king crab has been harvested in this region only in a subsistence fishery for which the catch limit has been 3 crabs per household per year. In this fishery, only male crabs with a carapace width >178 mm (or ~154 mm carapace length [CL]) may be taken legally (Orensanz et al., 1998). Crab pots or traps are used to capture red king crabs in this subsistence fishery. Harvest information has been available since 1995 for the Chiniak Bay area, which covers 321.0 km^2 and includes Womens Bay. With an area of 8.5 km^2, Womens Bay represents only about 2.5% of Chiniak Bay (Fig. 1). Harvest levels in Chiniak Bay from 1995 to 2012 ranged from 10 to 1178 crabs per year (median=66 crabs per year) (ADFG)[1] (Fig 2), which would indicate a low exploitation rate.

The population of red king crab in Womens Bay is not surveyed discretely, and no direct estimate of this population is available. However, the Kodiak district as a whole is surveyed by the Alaska Department of Fish and Game during its westward region trawl survey, when data are collected for estimates of the population size of red king crab and southern Tanner crab (*Chionoecetes bairdi*) in the northeast section of the Kodiak district, which includes Womens Bay (Fig. 1). For that survey ~90 tows are conducted, each 1.85 km long, in the northeast section of the Kodiak district with a 400-mesh eastern otter trawl constructed of 8.9-cm mesh in the body and 3.2-cm mesh in the codend to estimate population size by using the area-swept method (for complete survey methods and design, see Spalinger[2]).

Over the period of 1991–2012, estimates of the size of the population of red king crab in the northeast section have been low, ranging from about 160,000 to 0 (median=9500 crabs) (Fig. 2); these estimates are not precise because red king crabs typically are caught only at a few stations (Spalinger[2]). Our study area in Womens Bay accounts for <1% of the northeast section, a total area of 1978.5 km^2; therefore, the population in Womens Bay is likely a small proportion of the population estimated for this region.

[1] ADFG (Alaska Department of Fish and Game). 2012. Kodiak shellfish subsistence database. [Data available upon request from ADFG, 351 Research Ct, Kodiak, AK 99615-7400.]

[2] Spalinger, K. 2009. Bottom trawl survey of crab and groundfish: Kodiak, Chignik, South Peninsula, and Eastern Aleutians Management Districts, 2008. Fishery Management Report 9-25, 121 p. Alaska Department of Fish and Game, Anchorage, AK.

Materials and methods

Our study is based on a 17-year data set, from 1991 to 2008, of tracking red king crab in Womens Bay with acoustic tags. Crabs were tracked during other projects where behavior and habitat use by red king crab were examined (Dew et al., 1992; Dew and McConnaughey, 2005; Dew, 2010) and were found primarily in pods, which are aggregations of crabs (Dew, 1990). Red king crabs (identified per Donaldson and Byersdorfer, 2005) were captured by divers throughout Womens Bay, and acoustic tags (Sonotronics; Tucson, AZ[3]) were affixed to each crab's carapace with marine grade epoxy. Only active, healthy-looking crabs were used, and crabs typically were new-shell (i.e., they had recently molted).

Crabs were released from the surface at the same location where they were captured (Fig. 1). Tags emitted unique acoustic sequences, allowing for the identification and tracking of individual crabs, and tracking was performed from the surface with a Sonotronics USR-4D surface acoustic receiver deployed from a boat. Each time a crab was located, the position of the vessel at the sea surface above the crab was recorded with a GPS unit. Accuracy of the boat's location in relation to the crab's location was generally about 40 m and was dependent on depth and weather. Crabs also were tracked with a Datasonics DPL-275A, underwater acoustic dive receiver (Teledyne Benthos, North Falmouth, MA), which allows divers to use acoustic signals to locate tags in situ. Crabs were located on the seafloor by scuba divers, and data were collected on the behavior and habitat of all live, tagged crabs, and any closely aggregated crabs; data included whether crabs were trapped alive in ghostfishing gear.

We classified the final condition of all crabs that had been tagged, including crabs no longer attached to their tag, and recorded the status of unrecovered tags in the following manner. When a tag was found on a complete, newly shed carapace, the final condition of the crab was classified as "molted." When a tag was found attached to a dead or partially eaten crab, final condition of the crab was classified as "dead." When the condition of the crab could not be determined with any confidence, its condition was classified as "unknown." Tags that could not be located from the surface were recorded as "lost," indicating either that the tag had run out of power or had malfunctioned or that the crab had moved into an area where it could not be tracked. Because we tracked all tagged crabs until they died, molted, or became lost, no tagged crabs had their final condition classified as live (see the last paragraph of this section). When a crab was classified as dead, the cause of death was ascertained when possible. Ghostfishing-induced mortality (hereafter termed "ghostfishing mortality") was recorded when that crab was found dead in ghost-

[3] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

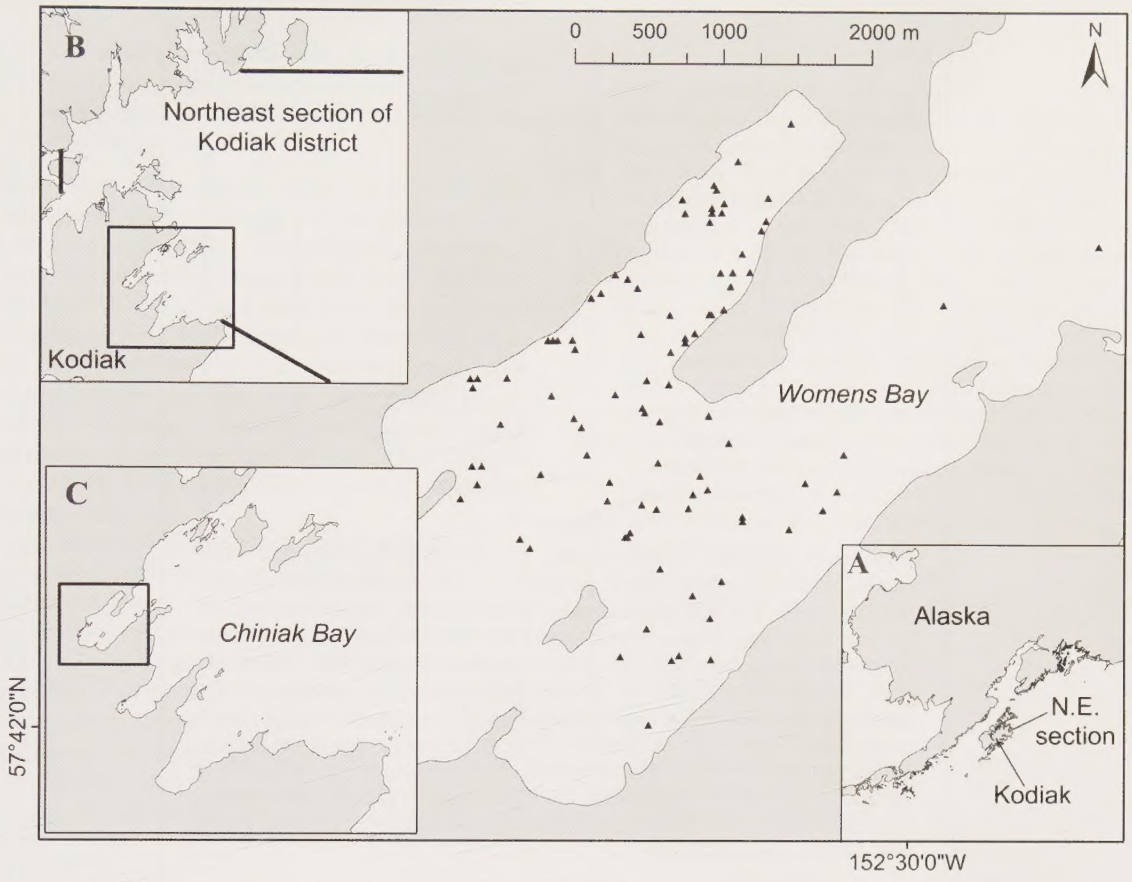

Figure 1

Map showing study area and sites (▲) where tagged red king crabs (*Paralithodes camtschaticus*) were released in Womens Bay, Kodiak Island, Alaska, during this study in association with other projects over the period of 1991–2008: (**A**) Alaska and Kodiak Island, (**B**) the northeast section of the Kodiak district, as defined for the westward region trawl survey of the Alaska Department of Fish and Game, and (**C**) Chiniak Bay. The southwestern portion of the bay is a shallow area where the red king crab does not occur, and no crabs were released there. In Inset A, lines are drawn to indicate Kodiak Island and the northeast section (N.E. section). In Inset B, lines show boundaries of the northeast section (adapted from the Fishery Management Report 09-25 by K. Spalinger published in 2009 by the Alaska Department of Fish and Game) and the rectangle around Chiniak Bay shows the extent of Inset C. In Inset C, the rectangle around Womens Bay shows the extent of the main map

fishing gear. On one occasion, 3 crabs released on the same day all died almost immediately for no apparent reason, and each of these crabs was recorded as a handling-induced mortality (hereafter "handling mortality"). There was no evidence of any latent handling mortality for other crabs in this study. All other causes of death were classified as "other mortality." One tag became detached from its crab because the epoxy failed to adhere to the carapace and was classified as a "tagging failure." Occasionally, surface tracking located a tag that had stopped moving for a long period of time and was not recovered because either it was in an unsuitable diving location or there were other logistical concerns (e.g., ice cover). Such tags were denominated as "derelict." Generally, all tagged crabs were tracked and diver observations were made weekly on a subset of tags, but effort varied with season, weather, and availability of field personnel.

When divers discovered ghost pots, both during this and other projects (effort on other projects varied throughout the study period) in Womens Bay, they made notes that included the type of gear, whether it was found intact or upside down, and the approximate number and species of crabs entangled or entrapped in the gear. Documentation of whether the pot was upside down is important because Dungeness pots have legally mandated biodegradable release mechanisms on their tops (ADFG[4]), making release ineffective if the

[4] ADFG (Alaska Department of Fish and Game). 2011. Shellfish gear requirements. Accessed September 2011. http://www.adfg.alaska.gov/index.cfm?adfg=personalusebyareasoutheastGear.main.

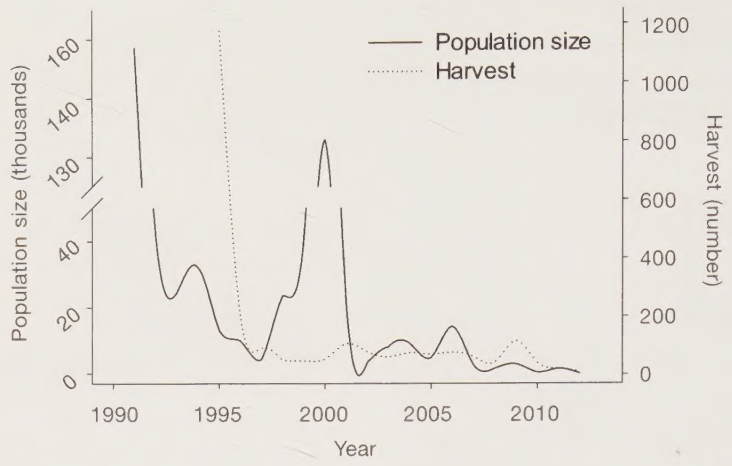

Figure 2

Population size and harvest levels for red king crab (*Paralithodes camtschaticus*) in 1991–2012. Population size (in thousands of individuals) is for the northeast section of the Kodiak district, as defined for the westward region trawl survey of the Alaska Department of Fish and Game, and harvest levels are for Chiniak Bay. The study area, Womens Bay, is part of Chiniak Bay, which is in turn part of the northeast section of Kodiak district (Fig. 1). Data used in this graph came from Alaska Department of Fish and Game reports on bottom trawl surveys of crabs and groundfishes conducted in 1991–2012: Technology Fishery Reports 93-16, 93-17 and Regional Information Report 4K95-1 by D. Urban, and Fishery Management Reports 05-48 and 13-27 by K. Spalinger.

pot is flipped over. Field personnel made observations on both ghost and actively fishing pots to determine the likely causes of pot loss in Womens Bay. Divers routinely disabled all ghost pots that they discovered, rendering them incapable of catching animals, and they released all trapped animals.

We assessed the effects of ghost fishing on the population of red king crab in Womens Bay by modeling the rate of tag loss. We assumed, on the basis of hundreds of hours of in situ observations during which we did not see any differences in behavior between tagged and untagged crabs, that tagged animals were representative of the population (except in cases of handling mortality, which we quantified and explicitly corrected for) and that tagging did not change behavior (Pollock et al., 1991). In particular, in the context of this study, we assumed that tagged crabs did not suffer higher natural or fishing mortality, that they did not molt at a higher rate, and that they were no more likely to enter a crab pot than were untagged crabs. Given these assumptions, the mortality rate of the population as a whole would be similar to the calculated mortality rates of tagged crabs (Pollock et al., 1991; Lambert et al., 2006).

As part of our determination of mortality rates, we estimated the number of days between the release date and date of final condition (e.g., the day a crab molted or died). If a tag had been located from the surface at the same position several times, then a dive was performed to determine the final condition of a crab. In most of these cases, we used the date from the second time the crab was located at that same position as the estimated date of final condition. When the time between the surface locations was greater than a month, the date half-way between them was used. If there was no indication that the crab had remained in the same location for a length of time (fewer than 2 surface observations at the same location), we used the day of the final dive observation as the end date.

We fitted the data using maximum likelihood to an exponential loss model assuming a binomial distribution such that

$$P = e^{-rt},$$

where P = the probability that a tagged crab molted, died, or was lost;
r = the instantaneous loss rate; and
t = the time in days.

We calculated the loss rate due to each cause (i.e., molting, ghostfishing mortality, handling mortality, or tag detachment, other mortality, and tag malfunction) with the proportional number of crabs in each category. For example, the rate of mortality from ghost fishing was calculated as

$$r_{GF} = rp_{GF},$$

where r_{GF} = the rate of crab loss due to ghost fishing;
r = the overall loss rate calculated above; and
p_{GF} = the proportion of crabs in this study that died from ghost fishing.

We assumed that tagged crabs with a condition classified as "unknown" had either died from causes other than ghost fishing (e.g., fishing mortality and poaching) or had molted. Additionally, we assumed that crab with tags classified as "derelict" had died from causes other than ghost fishing, had molted, or had been killed in ghostfishing gear. Therefore, we divided the crabs with unknown conditions or derelict tags into categories on the basis of the relative observed frequency of each cause of mortality. Tags classified as lost were kept as a separate category because no data on what happened to the tag were available.

Divers found 20 tagged crabs and hundreds of closely aggregated crabs alive in intact ghost pots and released them. In most cases, it was not possible to record the numbers of untagged live crabs released by divers because of the large numbers of those crabs and because visibility was greatly limited by silt disturbed from pot handling; therefore, only rough estimates were made. Two of the tagged crabs that were released later died in another crab pot. Given the length of time the crabs were likely in the pots, it is unlikely that many of these crabs would have escaped alive (High and Worlund, 1979).

To estimate an upper and lower limit for the mortality rate of crabs from ghost fishing in the absence of diver interference, we calculated the loss rates with the assumption that none of the crabs released from pots would have died (conservative estimate) and with the assumption that all of them would have died (upper estimate). For the conservative estimate, we used the date the crab died, molted, or was lost after having been released as the date of the final condition. For the upper estimate, we classified the crab as a "ghostfishing mortality" and used the date the crab was released from the pot as the date of the final condition of the crab, as if the crab had been found dead in the pot. We performed a logistic regression, using sex as a factor and CL as a covariate, to examine whether size or sex of a crab made it more likely that it would be caught or killed in ghostfishing gear.

Results

The size of tagged crabs ranged from 42 to 162 mm CL (mean=100 mm CL). Of the 192 crabs tagged over the course of multiple studies, 90 were female and 102 were male. The number of crabs tagged each year ranged from 2 (in 2007 and 2008) to 20 (in 1996) and averaged 11 crabs per year. Crabs were tracked for an average of 147 days and a maximum of 468. The total number of observations on tagged crabs was 3300. Molting was the most common final condition of a tagged crab, followed by unknown condition (Table 1). Three crabs migrated out of Womens Bay during the project, but they were tracked and their final condition was determined as was done for all other tagged crabs. Thirteen crabs died in ghostfishing gear, and 13 more crabs had other sources of mortality.

Table 1

Final conditions determined in this study for the 192 red king crabs (*Paralithodes camtschaticus*) or their tags that were tracked by acoustic tagging in association with other projects over the period of 1991–2008 in Womens Bay, Kodiak Island, Alaska. "Molted" means the tagged crab molted. "Unknown" means the tag was recovered by divers but it could not be determined if the tagged crab had molted or died. "Lost" means the tag could not be located from the surface. "Derelict" means the tagged crab either molted or died as evidenced by the fact the tag stopped moving but the condition was not determined by diving. "Other mortality" means the tagged crab died from a cause other than ghost fishing. "Ghostfishing mortality" means the tagged crab died in ghostfishing gear. "Handling mortality" means the tagged crab died as a result of the tagging process. "Tag failure" means the tag failed to adhere to the tagged crab's carapace.

Final condition	Number	Percentage
Molted	76	39.6
Unknown	48	25.0
Lost	22	11.5
Derelict	16	8.3
Other mortality	13	6.8
Ghostfishing mortality	13	6.8
Handling mortality	3	1.6
Tag failure	1	0.5

Known sources of mortality included predation by sea otters (3 crabs) and an octopus (1 crab) and likely poaching by humans (the tags of 2 crabs below the legal-size limit were returned to researchers with implausible stories about how the tags were obtained). Legal fishing did not account for a single mortality of a tagged crab during this study. Of the 13 crabs that died in ghostfishing gear, 12 crabs were caught in ghost pots and 1 crab was found in a ghost gill net. As for all the crabs caught in ghostfishing gear and released alive by divers, they all were found in the same type of gear: ghost pot.

Crabs that died in ghostfishing gear ranged from 69 to 160 mm CL and included 4 ovigerous females. Crabs caught and released by divers ranged from 66 to 141 mm CL and included 5 ovigerous females. One difference between the crabs that died and the crabs that were released was the number of days between the time when the crab was caught in the trap (as estimated from surface tracking) and the time when a

Table 2

Types of ghost pots found in Womens Bay, Kodiak Island, Alaska, by divers over the period of 1991–2008 and classification according to whether a pot was still intact and whether it was found upright or upside down. "Unknown" indicates that the type of pot could not be assessed. "Unknown condition" indicates that the divers could not determine if the pot was intact.

Type	Number found	Number intact	Percentage intact (%)	No. found upside-down	Unknown condition
Dungeness	70	46	66	8	2
Webbed	42	30	71	2	2
Home made	20	10	50	2	1
Store bought	7	3	43	1	2
Unknown	4	0	0	0	2
Total	143	89	62	13	9

dive was performed. The amount of time crabs spent in the trap averaged 38 (standard deviation [SD] 23 days) for crabs that died and 10 (SD 8 days) for crabs that were alive when released. The red king crab accounted for the majority of the organisms found in crab pots. Rarely found species included sculpins (*Myoxocephalus* spp.), southern Tanner crab, and Dungeness crab (*Metacarcinus magister*; *sensu* Schram and Ng, 2012).

Over the study period in Womens Bay, divers located 143 pots, of which 60 were found during the tracking of tagged crabs and 83 were found during other projects (Table 2). Of these pots, about half were Dungeness crab pots, which have the shape of a squat cylinder and a frame of steel covered with a mesh of stainless steel. Steel-frame pots, which are large, commercial-size pots with steel frames constructed in the shape of a pyramid, cone, or rectangle and which are covered in webbing that is usually made of nylon, were the next most frequently encountered type of pot, followed by home-made pots. Only a few sport pots, which are smaller, light-weight pots that are commercially produced and easily retrievable by hand, and pots of unknown type were found. Of the crab pots that were encountered, 62% were intact, indicating that those pots lacked a biodegradable release and were capable of ghost fishing. Additionally, other than the Dungeness crab pots, most of the pots lacked escape rings. Likely reasons for pot loss, determined on the basis of field observations, included release of a pot after a line was cut by boat propellers; entanglement of a pot in lines that were dragged by commercial barge towing bridals, sinking of a float due to biofouling on the lines, and breakage of a line by ice.

The conservative estimate of the overall rate of loss of tagged crabs from all sources, including sources of mortality, was about 10% less than the upper estimate; however, the upper estimate of the predicted mortality rate from ghost fishing was nearly 300% higher than the conservative estimate of the predicted mortality rate from ghost fishing (Table 3). Other sources of loss did not vary substantially between the 2 estimates. Overall annual mortality estimated from tagging data ranged from 40% to 56% for the conservative and upper estimates (Fig. 3). Using the calculated rate of mortality of tagged crabs in Womens Bay and applying it to the whole population of red king crab in this bay, we estimated that ghost fishing killed between 16% and 37% of the population per year, according to our conservative and upper estimates (Fig. 3).

Table 3

Instantaneous loss rates for tagged red king crabs (*Paralithodes camtschaticus*) and tags in Womens Bay, Kodiak Island, Alaska, during the period of 1991–2008. The conservative estimate for ghostfishing mortality was determined on the basis of counts of crabs that died in ghost-fishing gear. For the upper estimate, we assumed that all crabs caught in ghost-fishing gear and released by divers would have died. The estimate for experimental error includes handling mortality and tags that fell off crabs. The "All" category represents all sources of crab loss and is the parameter fitted by the exponential decay model (see the model in the *Materials and methods* section of the text for details). Standard errors of the mean are presented in parentheses.

	Loss rate ($days^{-1}$)	
Source of loss	Conservative	Upper
All	0.00709 (0.00003)	0.00782 (0.00004)
Molting	0.00476 (0.00017)	0.00466 (0.0003)
Ghostfishing mortality	0.00056 (0.00007)	0.00147 (0.00023)
Other mortality	0.00081 (0.00017)	0.00075 (0.00017)
Lost tag	0.00081 (0.00016)	0.00077 (0.00017)
Experimental error	0.00015 (0.00024)	0.00016 (0.00008)

Logistic regression revealed that neither size nor sex affected the probability of a tagged crab being killed or caught in ghostfishing gear, although there was a nonsignificant trend (P=0.055; Table 4) for larger (>140 mm CL) tagged crabs than for the smallest (40–60 mm CL) crabs to be killed in ghostfishing gear; however, this trend may be driven by the low number of crabs tagged in the smallest and largest size categories (Table 4, Fig. 4). Because we did not observe any ghostfishing mortality for crabs with CL ≤60 mm, we restrict our inference about the effect of ghost fishing at the population level to crabs with CL >60 mm. Although our data suggest that the ghostfishing mortality rate for the largest crabs (>140 mm CL; this size category includes legal-size crabs) is higher than our average rate for crabs of all sizes, we take the conservative approach by applying a constant rate of ghostfishing mortality to all crabs >60 mm CL because of our lower sample size for crabs in the largest size category.

Discussion

The 17-year data set used in our study allowed us to estimate the effect of ghost fishing on a local population of red king crab. The results of this study indicate that ghost fishing in Womens Bay was responsible for more mortality of red king crabs with CL >60 mm than any other single observed cause of mortality observed during our study. Indeed, our data provide evidence that the rate of mortality from ghost fishing may be almost double the rate from all other sources of mortality combined (for caveats to this assertion, see the discussion later in this section on mortality associated with molting). These results indicate that ghost fishing has a large, negative effect on the population of red king crab in Womens Bay and that changes in regulations designed to minimize ghost fishing or in their enforcement may be warranted.

Although many studies have quantified the effects of ghost fishing, most estimate the number of animals killed per unit of time (e.g., Breen, 1987; Hebert et al., 2001), the number killed per pot per unit of time (e.g., Bullimore et al., 2001; Al-Masroori et al., 2004; Campbell and Sumpton, 2009), or simply the number of crabs caught per pot (e.g., Stevens et al., 2000; Havens et al., 2008). These studies focus on following or recovering lost gear and examining catches and mortality over time on a local population. However, in scaling up to estimate effects on larger or commercially targeted populations, assumptions or estimates of the number of pots lost and the population size are required. By following the fates of individuals in the Womens Bay population, we could estimate with precision the actual mortality rate at the population level, assuming tags do not alter crab behavior. A drawback of this approach, however, is that it applies only to Womens Bay and is not easily extrapolated to other areas. Still, this problem is one shared by all studies of ghost fishing.

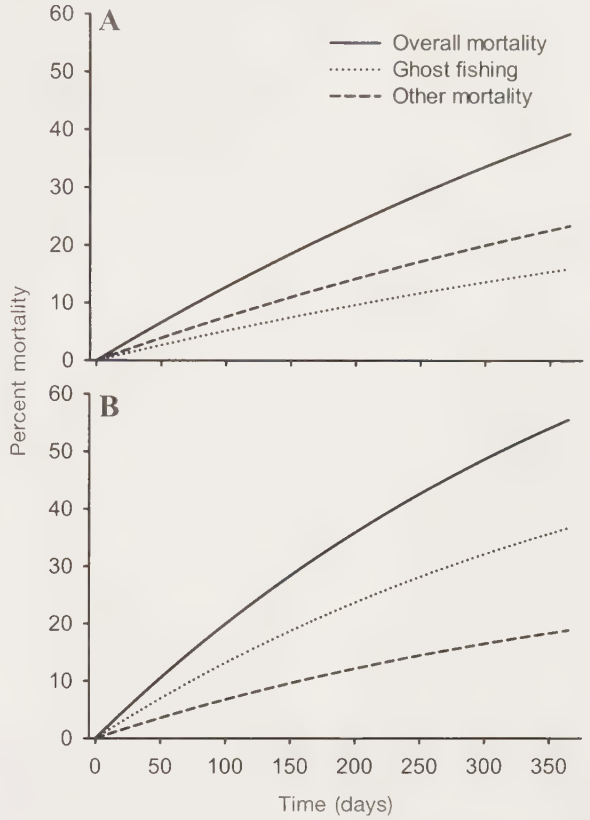

Figure 3

Predicted percent mortality over a year for red king crab (*Paralithodes camtschaticus*) in Womens Bay, Kodiak Island, Alaska. "Overall mortality" is the total mortality from all sources and is the sum of ghostfishing mortality and other mortality. "Ghost fishing" is the percentage of crabs that are killed in ghostfishing gear. "Other mortality" includes all other sources of mortality, including predation and fishing. (**A**) Conservative estimates of mortality; only crabs that died in ghostfishing gear were included in estimates of ghostfishing mortality. (**B**) Upper estimates of mortality; all crabs caught in intact ghostfishing gear were included in these estimates of ghostfishing mortality.

Our conservative estimate of ghostfishing mortality is precise, and because of the narrow definition for crabs considered to have died in pots, it represents the absolute minimum effect that ghost fishing had on the population of red king crab in Womens Bay during our study. However, it is likely a large underestimate. Because this study was not originally intended to document the effects of ghost fishing, divers actively decreased the effects of ghost fishing by releasing trapped crabs and disabling ghost pots. How many of the crabs caught in pots would have died is difficult to determine. Although escape rates for red king crabs from intact commercial red king crab pots may be up

Table 4

Results of logistic regression used to examine effects of size (carapace length) and sex on the likelihood of death or capture in ghostfishing gear for red king crabs (*Paralithodes camtschaticus*) in Womens Bay, Kodiak Island, Alaska, during the period of 1991–2008. *Z*=*Z*-score; *P*=probability. "Size" is the carapace length of the crab.

Parameter	Estimate	Standard error	*Z*	*P*
Crabs that died in ghostfishing gear				
Constant	–4.69	1.30	–3.61	0.000
Size	0.02	0.01	1.92	0.055
Sex (female)	–0.22	0.61	–0.37	0.714
Crabs that were caught in ghostfishing gear				
Constant	–2.57	0.82	–3.12	0.002
Size	0.01	0.01	0.89	0.373
Sex (female)	0.63	0.40	1.58	0.114

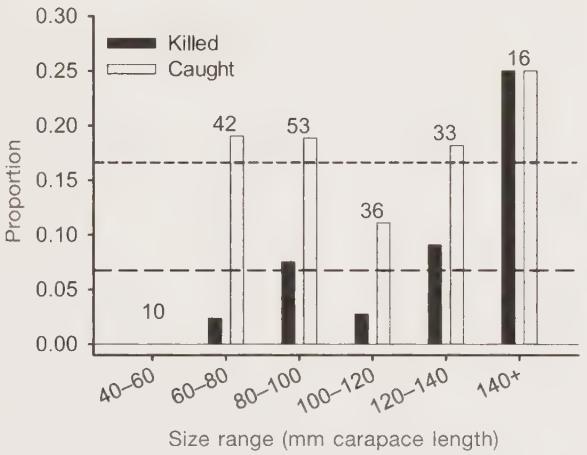

Figure 4

Proportion of tagged red king crabs (*Paralithodes camtschaticus*) that died (black bars) or were caught (gray bars) in ghostfishing gear in Womens Bay, Kodiak Island, Alaska, during the period of 1991–2008. Note that no crabs with carapace lengths between 40 and 60 mm were caught or killed. The number above each set of bars represents the total number of crabs in each size category. The line with the long dashes indicates the overall proportion of tagged crabs killed in ghostfishing gear, and the line with the short dashes indicates the overall proportion caught in ghostfishing gear.

to 90% (High and Worlund, 1979) and mortality of crabs trapped in such pots may be no higher than 17% (Godøy et al., 2003), these rates of escape and mortality do not reflect rates for most of the pots in our study because many of the pots observed in our study targeted the Dungeness crab.

Current regulations in Alaska require escape rings on Dungeness crab pots to be 121 mm, smaller than the 159 mm required for red king crab pots (ADFG[4]), but most of the pots found during our study that were of a type other than the Dungeness crab pot did not have escape rings. Therefore, we would expect much lower escape rates for red king crabs caught in the pots observed in this study. Estimates for mortality rates have been much lower for crabs trapped in red king crab pots than for crabs caught in many other pot types: 31–46% mortality of blue swimmer crabs (*Portunus pelagicus*) in blue swimmer crab pots (Campbell and Sumpton, 2009), 52% of Dungeness crabs in Dungeness crab pots (Breen, 1987), and 95% mortality of snow crabs (*Chionoecetes opilio*) in snow crab pots (Hebert et al., 2001).

Given the relatively small escape rings of pots designed for much smaller crab species and the absence of escape rings in the pots observed in this study, the majority of red king crabs found trapped in pots likely would have been unable to escape and eventually would have died. Results from our study suggest that red king crabs ≤60 mm CL are less likely to be caught or killed in pots than crabs of other sizes and that crabs >140 mm CL are more likely than crabs ≤140 mm to become trapped or to die in pots; however, these findings were not statistically significant and may have been driven to some extent by small sample sizes for crabs in the largest and smallest size categories. Although smaller crabs probably are more likely to escape from pots (High and Worlund, 1979), our data indicate that crabs >60 mm CL are vulnerable to the types of ghost pots observed in this study.

Escape of red king crabs from pots is asymptotic over time, and the number of crabs escaping levels off at about 8 days (High and Worlund, 1979). We estimated that only 8 of the 20 crabs released from pots had been trapped for less than 8 days. If the remaining 12 crabs had been able to escape, then they probably would have done so before they were rescued. Additionally, divers in this study actively disabled 89 intact pots that would otherwise have continued to ghost fish, likely substantially lowering the effect of ghost fishing in Womens Bay. Given these observations, we believe that the true mortality rate from ghostfishing gear is somewhere between our conservative and upper estimates and is most likely closer to the upper estimate.

Although our estimate of the rate of mortality of red king crabs from sources other than ghost fishing is reasonably precise, it is almost certainly an underestimate because it does not account for mortalities that may occur during molting, which is physiologically stressful

for crustaceans (Leffler, 1972), or shortly after molting, when they are particularly vulnerable to predation (Shirley et al., 1990; Ryer et al., 1997; Marshall et al., 2005). However, for the intermolt period of red king crab, our estimate is likely an accurate picture of mortality. Roughly a third of all crabs that died suffered predation, a sixth of them were poached, and the cause of death could not be determined for the remaining half. Ironically, no tagged male crabs of legal size were taken by fishermen in this study; no doubt, zero fishing mortality was due in part to the fact that few legal-size crabs were tagged and to the low fishing mortality for this species in the study area (Fig. 2). During another study in Bristol Bay, instantaneous mortality rates estimated for the red king crab ranged from 0.02 to 1.75 $year^{-1}$ and most estimates ranged between 0.02 and 1.00 $year^{-1}$ (reviewed in Zheng, 2005). Our estimates for rates of mortality from sources other than ghost fishing were 0.30 and 0.27 $year^{-1}$, values that fall well within that range.

The estimated mortality rate from ghost fishing is high enough to have a devastating effect on the population of red king crab in Womens Bay. A 60-mm-CL crab is at least 2 years from attaining reproductive maturity (Weber, 1967), and females must brood their eggs for a year after attaining maturity before they can reproduce successfully for the first time (Stevens and Swiney, 2007). Therefore, on the basis of our conservative and upper estimates of ghostfishing mortality (16–37% per year), we estimate, with the assumption that crabs become vulnerable to ghost fishing at a size of 60 mm CL, that 29–60% of male crabs and 41–75% of female crabs were killed in ghostfishing gear before they were able to reproduce for the first time during our study.

To put those high mortality rates in context, the target rate for fishing mortality designed to maintain a healthy stock size in Bristol Bay is <15% of the mature male biomass and only negligible numbers of nontargeted mature female and immature crabs are allowed to be taken as bycatch (Zheng and Siddeek[5]). Because the fecundity of females increases more than an order of magnitude with crab size (Swiney et al., 2012), ghost fishing keeps many females from reaching their full reproductive potential by killing them when they are small and have relatively low fecundity; moreover, because ghost fishing indiscriminately removes both immature and mature crabs, including ovigerous females, it compounds its effects as it reduces the reproductive capacity of the local population, as well as the size of the local population itself.

[5] Zheng , J., and M. S. M. Siddeek. 2010. Bristol Bay red king crab stock assessment in spring 2010. *In* Stock assessment and fishery evaluation report for the king and Tanner crab fisheries of the Bering Sea and Aleutian Islands regions. 2010 Crab SAFE, p. 135–246. North Pacific Fishery Management Council, Anchorage, AK. [Available from http://www.npfmc.org/wp-content/PDFdocuments/resources/SAFE/CrabSAFE/CRABSAFE2010.pdf.]

How typical Womens Bay may be among areas in the Gulf of Alaska is unknown. Its proximity to the city of Kodiak makes it a popular site for sport, subsistence, and commercial fisheries. The greater fishing effort and boat traffic in this bay, compared with such activities in other areas, has likely led to a higher rate of fishing gear loss. Additionally, participants in the sport and subsistence fisheries may be less likely to know about or comply with the requirements for escape mechanisms on pots. Supporting this premise, homemade pots found in our study were almost certainly not used for commercial purposes, and their structure was frequently noncompliant with established requirements for escape rings and biodegradable release. Enforcement of regulations in the sport and subsistence fisheries also probably is less stringent than it is in the commercial fishery because there are far fewer commercial fishermen to monitor (who fish with numerous pots per boat) than subsistence fishermen (who fish with few pots per boat). It is likely that other coastal bodies of water with high densities of crabs near population centers in Alaska have similar rates of ghost fishing and that bodies of water farther from human population centers have a lower rate.

If ghost fishing does have the profound effect that is indicated by our data on the population of red king crab in Womens Bay, measures to reduce ghost fishing are warranted. Of the different types of gear, crab pots were the major cause of ghostfishing mortality; in contrast, gill nets were responsible for only one death. Therefore, efforts to reduce ghost fishing on the red king crab should focus on pots (although removing nets may be a priority for other species, such as marine birds [Good et al., 2009; 2010]). Existing ghost pots can be located by side-scan sonar and removed by grappling (Stevens et al., 2000) and their threat eliminated as a result. Removal of ghost pots would be most effective in shallow areas of high fishing intensity, such as Womens Bay.

The observed effects of ice deserve a special note. Womens Bay frequently had a fresh water lens from various freshwater sources (Long, 1972) that can freeze during the winter. Ice embedded pot floats and when the ice broke up, pots were dragged into deeper water, where their float lines were not long enough to reach the surface, or they were dragged into shallow water, where pot owners were not likely to look for them. The strain of being dragged across the bottom of the bay could have caused lines to break. Additionally, tides or wind moved thin sheets of ice that abraded floats and lines and caused them to sink. Ice and boats dragged pots across the bottom of the bay, flipping some of them upside down or partially burying them—outcomes that, in the case of Dungeness crab pots, rendered the escape mechanism, if present, ineffective. If areas affected by ice were closed during months when ice was a concern, the rate of pot loss could be reduced. This closure would not substantially affect fishing because crab pots cannot be checked during times of ice cover.

Such closures also would reduce the number of pots abandoned and left out long enough to have their floats sunk by marine-fouling organisms.

Current regulations allow the tie-down of a pot lid to be equipped with cotton twine that will decay and release the lid after a length of time (ADFG[4]). However, we observed that pots can be flipped upside down when lost, rendering this escape mechanism unworkable. If Dungeness crab pots were required to have a sidewall release as an escape mechanism, this requirement would greatly reduce this problem. To reveal further means of reducing ghost fishing, more experimental work is needed to examine the effectiveness of various release mechanisms for allowing target species and other species to escape pots (Matsuoka et al., 2005).

Conclusions

Ghost fishing is an entirely wasteful source of mortality in aquatic systems. Although lost fishing gear is an inevitable consequence of fishing, it can become a substantial drain on both fished and nonfished species. In Womens Bay, ghost fishing, primarily by crab pots, is a source of mortality that may have a strong negative effect upon the population by killing 16–37% of the population per year. This negative effect could be decreased through implementation of measures to reduce the loss rate of crab pots and to ensure that pots do not continue to fish long after they are lost.

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Evaluation of a single nucleotide polymorphism baseline for genetic stock identification of Chinook Salmon (*Oncorhynchus tshawytscha*) in the California Current large marine ecosystem

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Abstract—Chinook Salmon (*Oncorhynchus tshawytscha*) is an economically and ecologically important species, and populations from the west coast of North America are a major component of fisheries in the North Pacific Ocean. The anadromous life history strategy of this species generates populations (or stocks) that typically are differentiated from neighboring populations. In many cases, it is desirable to discern the stock of origin of an individual fish or the stock composition of a mixed sample to monitor the stock-specific effects of anthropogenic impacts and alter management strategies accordingly. Genetic stock identification (GSI) provides such discrimination, and we describe here a novel GSI baseline composed of genotypes from more than 8000 individual fish from 69 distinct populations at 96 single nucleotide polymorphism (SNP) loci. The populations included in this baseline represent the likely sources for more than 99% of the salmon encountered in ocean fisheries of California and Oregon. This new genetic baseline permits GSI with the use of rapid and cost-effective SNP genotyping, and power analyses indicate that it provides very accurate identification of important stocks of Chinook Salmon. In an ocean fishery sample, GSI assignments of more than 1000 fish, with our baseline, were highly concordant (98.95%) at the reporting unit level with information from the physical tags recovered from the same fish. This SNP baseline represents an important advance in the technologies available to managers and researchers of this species.

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Chinook Salmon (*Oncorhynchus tshawytscha*) are found in rivers from central California around the North Pacific Rim and the Bering Sea to Russia and are the target of valuable commercial and recreational fisheries. A key aspect of the life history of Chinook Salmon is natal homing, whereby each fish of this anadromous species typically returns to spawn in the same river in which it was born. This homing generates populations (or stocks) that may be genetically differentiated from neighboring populations and can exhibit local adaption (Utter et al., 1989; Taylor, 1991). Recent population declines, particularly at the southern end of the native range of this species, have resulted in the listing of many stocks under the U.S. Endangered Species Act (ESA; Federal Register, 1990, 1999) and have highlighted the need to refine the management and conservation of Chinook Salmon. However, such refinements are challenging because the migratory life history of salmon means that the many effects from anthropogenic sources that occur in rivers or in the ocean (e.g., fisheries, water diversion, or turbine entrainment) may affect multiple, intermingled stocks. In such cases, it may be necessary to discern the stock of origin of affected fish to monitor stock-specific impacts and design management strategies accordingly.

The use of pre-existing biological markers to distinguish salmon stocks has a long history. The traits used in these efforts have included morphometric and meristic characters (Fournier et al., 1984; Claytor and MacCrimmon, 1988), scale patterns (Cook, 1982), parasite assemblages (Boyce et al., 1985), and stable isotope ratios (Barnett-Johnson et al., 2008). However, the most universally applicable methods have involved the use of genetic markers because every fish has a unique genetic makeup. The first genetic markers widely used for identification in salmon were electrophoretically detectable protein polymorphisms known as allozymes (Milner et al., 1985; Shaklee and Phelps, 1990; Tessier et al., 1995; Allendorf and Seeb, 2000). With the advent of polymerase chain reaction (PCR), many more types of genetic markers became available to

discriminate salmon populations, including mitochondrial DNA polymorphisms (Cronin et al., 1993), minisatellites (Beacham et al., 1996; Miller et al., 1996), microsatellites (Seeb et al., 2007; Moran et al., 2013), amplified-fragment length polymorphisms (Flannery et al., 2007) and, most recently, single nucleotide polymorphisms (SNPs; Smith et al., 2005a, 2005b; Aguilar and Garza, 2008; Narum et al. 2008; Abadía-Cardoso et al., 2011; Clemento et al., 2011).

Genetic stock identification (GSI) typically proceeds in 2 steps. First, samples are collected from potential source populations and genotyped with a set of genetic markers in order to estimate population allele frequencies. These genotypes are called the "baseline." Then, data from individuals sampled from a mixed-stock collection (called a "mixture") and genotyped with the same set of genetic markers are compared with the baseline to estimate the relative proportions of individuals that came from each of the represented source populations. Single individuals of unknown origin also can be assigned to specific populations. Maximum likelihood or Bayesian methods typically are used to carry out GSI inference (Smouse et al., 1990; Pella and Masuda, 2000).

For the first large-scale baseline for GSI of Chinook Salmon allozyme markers were used (Teel et al.[1]), but technical and logistical issues limited their future appeal. The allozyme database was supplanted in Canada by a microsatellite baseline developed by the Department of Fisheries and Oceans (Beacham et al., 2006) and more broadly by a microsatellite baseline database developed through a large, international collaboration (Seeb et al., 2007). This collaboration required enormous effort to standardize data across laboratories because microsatellite allele names and sizes usually are not consistent between different laboratories and genotyping equipment.

The Seeb et al. (2007) microsatellite baseline has been an effective tool for GSI but has a number of disadvantages: genotyping and scoring of microsatellites is labor-intensive; genotyping error rates can be relatively high, making the 13 microsatellites in that baseline inadequate for applications such as pedigree reconstruction (Anderson and Garza, 2006; Garza and Anderson[2], Abadía-Cardoso et al., 2013); missing data rates also can be quite high; and, finally, any new laboratory that wishes to use that baseline must undertake a costly standardization process. Additionally, it now has been demonstrated that SNPs, despite typically having only 2 alleles per locus, do have sufficient power to be employed successfully in a GSI context with a modest number of genetic markers (Smith et al., 2007; Narum et al., 2008; Templin et al., 2011; Larson et al., 2013).

Early simulation studies indicated that the bi-allelic nature of SNPs would make them less useful than highly polymorphic microsatellites for population discrimination (Bernatchez and Duchesne, 2000; Kalinowski, 2004). However, SNPs are located throughout the genome and may be discovered in genetic regions with higher than average divergence (Nosil et al., 2009), increasing their utility for GSI. Moreover, SNPs do not suffer from many of the disadvantages of using microsatellites: SNP markers are amenable to the automated, high-throughput genotyping required for large projects; SNP genotyping error rates are very low, making them suitable for pedigree reconstruction; and, importantly, SNP assays typically do not require standardization between labs and, therefore, a SNP baseline is immediately useful to any group or agency that genotypes a mixture sample with the markers used in that baseline (Seeb et al., 2011).

Here, we describe the development and evaluation of a new baseline of SNP marker data for Chinook Salmon in the southern part of their native range for use in ecological investigation in the California Current large marine ecosystem (and its tributaries) and in fisheries managed by the Pacific Fishery Management Council (PFMC). We introduce a panel of 96 SNP markers and a baseline of more than 8000 salmon from 68 populations of Chinook Salmon ranging from California to Alaska and a single collection of Coho Salmon (*Oncorhynchus kisutch*) from California. We describe the procedures used to select these SNP markers from among a larger number of candidates and document the resulting patterns of genetic differentiation between various populations. We evaluate the power of this new baseline for GSI by both self-assignment (genetic identification of the most likely population of origin) and simulated mixture analyses, focusing on stocks commonly encountered in PFMC fisheries. Finally, we analyze 2090 fish sampled in 2010 from the sport and commercial fisheries off the coast of California and compare the results of these analyses with the coded wire tag (CWT) data from these fish to demonstrate the effectiveness of this baseline for classifying individuals to specific management units.

Materials and methods

Baseline populations

Populations were selected for inclusion in the new baseline to provide broad geographic coverage across

[1] Teel, D. J., P. A. Crane, C. M. Guthrie III, A. R. Marshall, D. M. Van Doornik, W. Templin, N. V. Varnavskaya, and L. W. Seeb. 1999. Comprehensive allozyme database discriminates Chinook salmon around the Pacific Rim. NPAFC document 440, 25 p. [Available from Alaska Department of Fish and Game, Division of Commercial Fisheries, 333 Raspberry Rd., Anchorage, AK 99518.]

[2] Garza, J. C., and E. C. Anderson. 2007. Large scale parentage inference as an alternative to coded-wire tags for salmon fishery management. *In* PSC genetic stock identification workshop: Logistics Workgroup final report and recommendations; Portland, OR, 15–17 May 2007 and Vancouver, Canada, 11–13 September 2007, p. 48–55 p. [Available from Pacific Salmon Commission, 600-1155 Robson St., Vancouver, BC V6E 1B5, Canada.]

the range of Chinook Salmon in the the United States from Washington to California, while also allowing for the identification of fish from elsewhere in the geographic range of this species. Adult fish were sampled on spawning grounds, in terminal fisheries, or at hatcheries during the period of 2003–13 and were provided by numerous contributors (see the *Acknowledgments* section and Warheit et al.[3]). We included populations expected to be encountered in ocean fisheries off California and Oregon, as well as populations with special management status (e.g., ESA-listed populations). Accordingly, the major lineages of Chinook Salmon from California and Oregon were emphasized in this baseline, as were populations distinguished by life history strategy (e.g., spring-run, fall-run, and winter-run strategies), but representatives of the major lineages from farther north also were included.

DNA was extracted from samples for California populations with DNeasy Blood & Tissue Kits on a BioRobot 3000[4] platform (QIAGEN, Inc., Valencia, CA) according to the manufacturer's protocols, and DNA from populations in Oregon, Washington, Canada, and Alaska was extracted by contributors (see *Acknowledgments* section) who used various methods. Sample sizes ranged from 44 to 1409 individuals per population and averaged 116 individuals per population. The 1409 fish from the population in the Trinity River Hatchery initially were genotyped with our SNP panel for another purpose, but they were included here in total to provide a comprehensive reference sample for identification of this important group. Excluding this disproportionately large sample, the average number of individuals per population was 97. In total, the new baseline included 7984 Chinook Salmon from 68 distinct populations (Table 1).

Each population in this baseline belongs to a single reporting unit, a designation established in previous GSI research that reflects a combination of "genetic similarity, geographic features, and management applications" (Seeb et al., 2007). Reporting units generally are composed of multiple populations that share genetic similarity or are subject to similar management regimes. The 68 populations of Chinook Salmon in our baseline fall into 38 distinct reporting units (Table 1), and some reporting units in Alaska and Canada are represented by only a single population.

Coho Salmon occasionally are misidentified as Chinook Salmon in ocean fisheries and in ecological sampling. We included a collection of 47 Coho Salmon from California as the 69th population in our baseline to help us to identify Coho Salmon that have been identified incorrectly as Chinook Salmon.

Markers and genotyping

We compiled a list of 192 TaqMan (Life Technologies Corp., Carlsbad, CA), or 5'-nuclease, SNP genotyping assays from previously published discovery studies (Smith et al., 2005a, 2005b; Campbell and Narum, 2008; Narum et al., 2008; Clemento et al., 2011) to test their scorability and power for GSI. TaqMan technology combines standard PCR primers that target the genomic region around a SNP with 2 different fluorescent probes that identify the 2 nucleotide bases present at the SNP. As recommended by the manufacturer, we used a multiplex preamplification reaction to increase the copy number of targeted genomic regions. Multiplex PCR products were diluted with 15 μL of 2 mM Tris buffer and were frozen.

Samples then were genotyped on 96.96 Dynamic Arrays with an EP1 System (Fluidigm Corp., South San Francisco, CA) according to the manufacturer's protocols. Fluidigm Dynamic Arrays use integrated nanofluidic circuitry to simultaneously determine the genotype at 96 SNP loci for 96 samples (2 of which are no-DNA template controls). Genotypes were determined with the Fluidigm Genotyping Analysis software (vers. 2.1.1). The use of quantitative PCR methods for genotype determination involves discerning, on a 2-D graph, clusters of fluorescence intensity of the probes for the 2 alleles; the 2 homozygote clusters have fluorescence primarily from only 1 probe, but a heterozygote cluster has similar intensities from both probes.

Marker selection

We selected a panel of 95 SNP markers from among the 192 candidates, reserving 1 marker for a species identification assay (see final paragraph of this section). The risk of "high-grading bias" (i.e., wrongly inflating the apparent resolving power of a group of loci for GSI) is particularly great when selecting a panel of markers to distinguish between populations that are closely related, as many of the populations in our baseline are. To avoid high-grading bias, we employed the "training-holdout-leave-one-out" (THL) procedure of Anderson (2010); this procedure requires that data be split into training and holdout sets. Training-set genotypes are used to select the loci included in a baseline and can be included in the eventual baseline, but they are not used to evaluate its performance. Rather, performance of a baseline is determined with simulation and self-assignment with only the holdout set, which was not used in any way to select baseline loci. We chose a training set of 372 individuals drawn from 22 populations (14 from California, 3 from Oregon, 3 from Washington, 1 from British Columbia, and 1 from Alaska) for initial genotyping with all 192 loci.

[3] Warheit, K. I., L. W. Seeb, W. D. Templin, and J. E. Seeb. 2013. Moving GSI into the next decade: SNP coordination for Pacific Salmon Treaty fisheries. FPT 13-09, 47 p. [Available from Washington Department of Fish and Wildlife, 600 Capitol Way N., Olympia, WA 98501-1091.]

[4] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 1

Populations and reporting units in the single nucleotide polymorphism baseline for genetic stock identification of Chinook Salmon (*Oncorhynchus tshawytscha*) from the west coast of North America. Shown are the names used on the phylogeographic tree (Fig. 1), the total number of individuals sampled (n), the number used in the training set (n_{train}), estimates of unbiased (Unb.) and observed (Obs.) heterozygosity (Hz), and the mean number of alleles (A); also shown are the proportion of individuals that self-assign (Assign.) to the population (pop.) from which they were sampled and the proportion that self-assign to the correct reporting (rep.) unit, as well as the mean F_{ST} for each population within and between reporting units. The slash (/) in reporting unit names indicates the inclusion of multiple run types (e.g. summer and fall) or geographic regions (e.g. North California and South Oregon) in the same reporting unit. Note that mean summary values shown were calculated excluding the sample of Coho Salmon (*Oncorhynchus kisutch*). The use of "spring," "summer," "fall," or "winter" in a unit or population name specifies to which run it belongs. N. = Northern; S. = Southern; R. = River; Up. = upper; Hatch. = Hatchery.

Reporting unit	Population	Tree name	n	n_{train}	Unb. Hz	Obs. Hz	A	Assign. to pop.	Assign. to rep. group	Mean F_{ST} within	Mean F_{ST} between
Central Valley spring	Butte Creek spring	CVsp_Butte	425	26	0.357	0.330	1.99	0.68	0.93	0.017	0.196
	Mill Creek spring	CVsp_Mill	145	23	0.371	0.377	1.99	0.48	0.80	0.012	0.173
	Deer Creek spring	CVsp_Deer	119	12	0.367	0.346	1.99	0.50	0.80	0.013	0.174
	Up. Sacramento R. spring	CVsp_UpSac_late	372	–	0.368	0.355	1.99	0.26	0.78	0.008	0.175
Central Valley fall	Feather R. Hatchery spring	CVfl_FeatherRHsp	470	47	0.373	0.374	1.99	0.44	0.87	0.009	0.179
	Feather River Hatchery fall	CVfl_FeatherRHfl	146	23	0.370	0.371	1.98	0.18	0.85	0.004	0.190
	Butte Creek fall	CVfl_Butte	188	–	0.369	0.355	2.00	0.13	0.91	0.003	0.187
	Mill Creek fall	CVfl_Mill	97	12	0.366	0.358	1.98	0.14	0.95	0.004	0.200
	Deer Creek fall	CVfl_Deer	70	–	0.363	0.347	1.98	0.29	0.90	0.005	0.195
	Mokelumne River fall	CVfl_Mklmne	95	27	0.370	0.373	1.98	0.26	0.94	0.005	0.198
	Battle Creek fall	CVfl_Battle	141	23	0.369	0.351	1.99	0.29	0.89	0.005	0.188
	Up. Sacramento R. late-fall	CVfl_UpSac	93	23	0.367	0.364	2.00	0.54	0.93	0.010	0.193
Central Valley winter	Sacramento River winter	Sac_win	295	19	0.297	0.289	1.97	1.00	1.00	–	0.263
California Coast	Eel River	CACoast_Eel	95	12	0.327	0.321	2.00	0.89	0.96	0.029	0.203
	Russian River	CACoast_Russian	94	–	0.368	0.372	2.00	0.84	0.98	0.029	0.156
Klamath River	Klamath Iron Gate Hatchery	Klamath_IronGH	117	12	0.326	0.345	1.97	0.97	0.99	0.053	0.232
	Trinity River Hatchery	Klamath_TrinityHsp	1409	12	0.318	0.312	2.00	0.93	0.97	0.053	0.243
North California/ South Oregon Coast	Smith River	nCal_sOR_Smith	159	–	0.377	0.381	1.99	0.77	0.87	0.014	0.138
	Chetco River	nCal_sOR_Chetco	94	11	0.372	0.367	1.99	0.73	0.86	0.014	0.137
Rogue River	Cole Rivers Hatchery	Rogue_ColeRHsp	141	11	0.367	0.362	2.00	0.62	0.86	0.006	0.155
	Applegate Creek	Rogue_Applgt	92	–	0.369	0.361	2.00	0.50	0.77	0.006	0.153
Mid Oregon Coast	Coquille River	mOR_Coquille	47	–	0.352	0.343	1.99	0.72	0.83	0.039	0.151
	Umpqua River spring	mOR_Umpqua	137	11	0.386	0.375	2.00	0.63	0.64	0.055	0.119
	Siuslaw River	mOR_Siuslaw	93	–	0.345	0.348	1.98	0.40	0.46	0.040	0.146
North Oregon Coast	Nestucca Hatchery	nOR_NestuccaH	48	–	0.338	0.328	1.96	0.71	0.83	0.029	0.160
	Alsea River	nOR_Alsea	131	–	0.335	0.309	2.00	0.47	0.76	0.042	0.159
	Nehalem River	nOR_Nehalem	93	–	0.316	0.317	1.96	0.97	0.99	0.059	0.193
	Siletz River	nOR_Siletz	93	–	0.331	0.330	1.98	0.69	0.81	0.031	0.163

Table 1 (cont.)

Populations and reporting units in the single nucleotide polymorphism baseline for genetic stock identification of Chinook Salmon (*Oncorhynchus tshawytscha*) from the west coast of North America. Shown are the names used on the phylogeographic tree (Fig. 1), the total number of individuals sampled (n), the number used in the training set (n_{train}), estimates of unbiased (Unb.) and observed (Obs.) heterozygosity (Hz), and the mean number of alleles (A); also shown are the proportion of individuals that self-assign (Assign.) to the population (pop.) from which they were sampled and the proportion that self-assign to the correct reporting (rep.) unit, as well as the mean F_{ST} for each population within and between reporting units. The slash (/) in reporting unit names indicates the inclusion of multiple run types (e.g. summer and fall) or geographic regions (e.g. North California and South Oregon) in the same reporting unit. Note that mean summary values shown were calculated excluding the sample of Coho Salmon (*Oncorhynchus kisutch*). The use of "spring," "summer," "fall," or "winter" in a unit or population name specifies to which run it belongs. N. = Northern; S. = Southern; R. = River; Up. = upper; Hatch. = Hatchery.

Reporting unit	Population	Tree name	n	n_{train}	Unb. Hz	Obs. Hz	A	Assign. to pop.	Assign. to rep. group	Mean F_{ST} within	Mean F_{ST} between
Willamette River	North Santiam Hatchery	Willamette_NSantiamH	93		0.324	0.327	1.95	0.80	0.99	0.014	0.181
	McKenzie Hatchery	Willamette_McKenzHsp	48	–	0.334	0.376	1.94	0.69	0.96	0.014	0.175
Deschutes fall	Lower Deschutes River	Deschutes_fl	94		0.366	0.357	2.00	0.56	0.56	–	0.145
Lower Columbia fall	Cowlitz Hatchery fall	COlow_CowHfl	141	–	0.365	0.374	1.99	0.79	0.79	–	0.142
Lower Columbia spring	Cowlitz Hatchery spring	COlow_CowHsp	44	11	0.368	0.370	1.97	0.67	0.70	0.029	0.160
	Kalama Hatchery spring	COlow_KalamaHsp	48	12	0.372	0.359	1.99	0.50	0.61	0.029	0.134
Mid Columbia Tule fall	Spring Creek Hatchery	COmid_SpringCH	142	–	0.322	0.331	1.97	0.97	0.97		0.206
Upper Columbia summer/fall	Hanford Reach	COup Hanford	92	–	0.355	0.353	1.99	0.36	0.76	0.002	0.166
	Priest Rapids Hatchery	COup_PriestHsumfl	48	–	0.361	0.359	1.99	0.25	0.83	0.002	0.164
	Wells Hatchery	COup WellsHsumfl	48	–	0.355	0.369	1.99	0.46	0.92	0.004	0.175
Mid and Upper Columbia spring	Wenatchee River	COmup_Wenatchee	48	–	0.209	0.202	1.88	0.85	0.85	0.048	0.260
	Cle Elum Hatchery	COmup_CleEHsp	48	–	0.262	0.255	1.95	0.94	0.96	0.048	0.219
Snake River fall	Lyons Ferry Hatchery	Snake_LyonsFHfl	119	12	0.359	0.360	2.00	0.45	0.45	–	0.158
Snake River spring/summer	Rapid River Hatchery	Snake_RapidRHsumsp	48	–	0.191	0.194	1.84	0.85	0.94	0.034	0.272
	McCall Hatchery	Snake_MCallHsumsp	48	–	0.199	0.196	1.84	0.75	0.96	0.034	0.278
Washington Coast	Forks Creek Hatchery	WACoast ForksCH	93	–	0.350	0.345	1.99	0.89	0.94	0.042	0.143
	Quinalt Lake fall	WACoast_Quinalt	48	–	0.348	0.341	1.98	0.90	0.96	0.042	0.152
South Puget Sound	Soos Creek Hatchery	sPuget SoosCH	142	–	0.360	0.358	2.00	0.91	0.91	–	0.158
North Puget Sound	Kendall Hatchery spring	nPuget_KendlHsp	48	–	0.326	0.336	1.95	0.92	0.96	0.042	0.170
	Marblemount Hatch. spring	nPuget_MrblHsp	48	–	0.343	0.337	1.99	0.92	0.94	0.042	0.156
Lower Fraser	Harrison River	Fraser_Harris	48	–	0.329	0.326	1.98	0.96	0.96	0.152	0.169
	Birkenhead Hatchery	Fraser_BirkenH	91	–	0.259	0.255	1.84	1.00	1.00	0.152	0.231
Lower Thompson River	Spius Creek Hatchery	Thompson_SpiusCH	46	11	0.271	0.275	1.89	1.00	1.00	–	0.201
East Vancouver Island	Big Qualicum Hatchery	eVancI_BigQual	48	–	0.352	0.338	2.00	0.83	0.83	–	0.145

Table 1 (cont.)

Populations and reporting units in the single nucleotide polymorphism baseline for genetic stock identification of Chinook Salmon (*Oncorhynchus tshawytscha*) from the west coast of North America. Shown are the names used on the phylogeographic tree (Fig. 1), the total number of individuals sampled (n), the number used in the training set (n_{train}), estimates of unbiased (Unb.) and observed (Obs.) heterozygosity (Hz), and the mean number of alleles (A); also shown are the proportion of individuals that self-assign (Assign.) to the population (pop.) from which they were sampled and the proportion that self-assign to the correct reporting (rep.) unit, as well as the mean F_{ST} for each population within and between reporting units. The slash (/) in reporting unit names indicates the inclusion of multiple run types (e.g. summer and fall) or geographic regions (e.g. North California and South Oregon) in the same reporting unit. Note that mean summary values shown were calculated excluding the sample of Coho Salmon (*Oncorhynchus kisutch*). The use of "spring," "summer," "fall," or "winter" in a unit or population name specifies to which run it belongs. N. = Northern; S. = Southern; R. = River; Up. = upper; Hatch. = Hatchery.

Reporting unit	Population	Tree name	n	n_{train}	Unb. Hz	Obs. Hz	A	Assign. to pop.	Assign. to rep. group	Mean F_{ST} within	Mean F_{ST} between
West Vancouver Island	Robertson Hatchery	wVancI_RobHfl	48	-	0.341	0.364	1.98	0.96	0.96	–	0.152
Lower Skeena River	Lower Kalum River	lSkeena_Kalum	48	-	0.303	0.303	1.96	0.77	0.77		0.156
Mid Skeena River	Morice River	mSkeena_Morice	47		0.279	0.276	1.89	0.81	0.91	0.013	0.173
	Kitwanga River	mSkeena_Kitwanga	48	-	0.291	0.290	1.94	0.54	0.75	0.013	0.175
S. Southeast Alaska	Little Port Walter - Unuk	sSEAK_Unuk	48	–	0.301	0.290	1.94	0.79	0.79	–	0.165
Alsek River	Goat Creek	AlsekAK_Goat	48	–	0.243	0.245	1.69	0.96	0.96	–	0.248
Karluk River	Karluk River	KarlukAK	47	–	0.230	0.220	1.73	1.00	1.00	–	0.237
Taku River	Little Tatsamenie Lake	Taku_LilTats	48	–	0.271	0.265	1.92	0.90	0.90	-	0.188
Chilkat River	Pullen Creek Hatchery	nSEAK_PullenCH	48	–	0.260	0.276	1.77	0.98	0.98	–	0.209
Situk River	Situk River	SitukAK	48	12	0.244	0.248	1.77	0.94	0.94	–	0.210
Copper River	Sinona Creek	CopperAK_Sinona	47	–	0.229	0.226	1.63	0.98	0.98		0.244
Susitna River	Montana Creek	SusitnaAK_Montana	48	–	0.210	0.201	1.73	0.92	0.92		0.249
Western AK, Lower	George River	WestAK_George	47		0.234	0.229	1.78	0.43	0.98	0.004	0.239
Kuskokwim River	Kanektok River	WestAK_Kanektok	48	–	0.241	0.232	1.81	0.38	0.96	0.001	0.233
	Togiak River	WestAK_Togiak	48	–	0.241	0.229	1.79	0.40	0.94	0.005	0.233
Yukon River	Kantishna River	Yukon_Kantishna	48	–	0.208	0.204	1.67	0.94	0.94	–	0.269
Coho Salmon	California Coho	Coho	47	-	0.089	0.094	1.33	1.00	1.00	-	0.463
		total	8031	mean	0.320	0.317	1.93	0.69	0.88	0.028	0.188

For each locus, k, the observed relative frequencies, p_{ik} and q_{ik}, of the 2 SNP alleles were calculated for each population, i, in the training set. These values then were used to compute the expected probability of misassignment, $P(\text{Mis}_{ijk})$, between every pair of populations i and j with only a single locus k:

$$P(\text{Mis}_{ijk}) = 0.5\ [\delta(p_{ik} \leq p_{jk}) p_{ik}^2 + \delta(p_{ik}q_{ik} \leq p_{jk}q_{jk}) 2p_{ik}q_{ik} + \delta(q_{ik} \leq q_{jk}) q_{ik}^2 +$$

$$\delta(p_{ik} \geq p_{jk}) p_{jk}^2 + \delta(p_{ik}q_{ik} \geq p_{jk}q_{jk}) 2p_{jk}q_{jk} + \delta(q_{ik} \geq q_{jk}) q_{jk}^2],$$

for all k where $\delta(x) = 1$ if the condition x is true and 0 if otherwise.

The values of $P(\text{Mis}_{ijk})$ were used to rank the loci for their suitability for resolving between populations i and j in GSI; a lower $P(\text{Mis}_{ijk})$ indicates better resolving power.

The rankings derived from $P(\text{Mis}_{ijk})$ values were combined with other criteria in a nonautomated process to select the final panel of loci (Table 2). Each SNP assay was evaluated for scorability and evidence of Hardy-Weinberg disequilibrium and linkage disequilibrium (LD). Assays with overly dispersed clusters, more than 3 clusters, or inadequate spacing between clusters were excluded. Loci with significant deviations from equilibrium expectations also were removed. SNPs with large differences in allele frequencies between populations are particularly effective for GSI, whereas SNPs with high minor allele frequencies (MAFs) are most useful for parentage analysis (Anderson and Garza, 2006).

The remaining 168 loci were then ranked by their MAFs in hatchery populations to be included in pedigree reconstruction studies (see *Discussion* section). Previous simulations indicated that about 100 loci with an MAF >0.2 would be required to achieve the necessary statistical power to assign parentage with sufficiently low false-negative and false-positive rates (Anderson and Garza, 2006). However, the observed MAFs for many loci were in fact >0.2 (and as high as 0.5), indicating that the desired statistical power could be achieved with fewer loci. Therefore, we selected the 70 loci with the highest MAF in the Feather River population, the primary target for subsequent parentage investigations. We then used the $P(\text{Mis}_{ijk})$ rankings to select 25 additional loci that were useful for distinguishing between difficult-to-resolve populations and reporting units. Finally, an assay to discriminate between Chinook and Coho salmon was included as the 96th assay for genotyping with the Fluidigm 96.96 Dynamic Arrays.

Population genetics analyses

The 7669 samples that were not in the training set for locus selection were genotyped with the final panel of 96 SNPs and used as the holdout set in subsequent power analyses (see the next section). This holdout set also was used for standard population genetics analyses. We tested each locus-population pair for deviations from Hardy-Weinberg equilibrium (HWE) with the complete enumeration method (Louis and Dempster, 1987) in GENEPOP software, vers. 4.0 (Rousset, 2008). Similarly, in each population, all pairwise locus combinations were investigated for LD. Default Markov chain parameters were used, except for the number of batches, which was increased to 500 to reduce the standard error to acceptable levels (<0.02; Rousset, 2008).

Genetic differentiation (F_{ST}) was estimated (with θ of Weir and Cockerham, 1984) between all pairs of populations with the software package GENETIX, vers. 4.05 (Belkhir[5]). The data set was permuted 1000 times to determine the significance of F_{ST} estimates. Phylogeographic trees were constructed with the chord distance (DCE) of Cavalli-Sforza and Edwards (1967) and the neighbor-joining algorithm in the software package PHYLIP, vers. 3.69 (Felsenstein[6]) and were visualized with Dendroscope software, vers. 3.2.10 (Huson et al., 2007). Majority-rule consensus values were calculated from 10,000 bootstrap samples of the data through the use of the PHYLIP component CONSENSE. The F_{ST} values and genetic distances computed are expected to provide an inflated estimate of the isolation between populations because the SNP loci used in our analyses were not a random sample from the genome; some SNP loci were chosen for their power in resolving specific population pairs in our baseline. Nonetheless, these estimates are useful for assessment of the relative genetic differentiation among the populations described here.

Power analyses

We used 3 different methods to assess the power of the SNP baseline for GSI. First, we performed a self-assignment analysis, and subsequently we generated and analyzed simulated mixtures with 2 different procedures.

In self-assignment analysis, allele frequencies for each potential source population generally are estimated from the samples. Then, for each individual, the probability that its genotype would occur in each population (assuming Hardy-Weinberg and linkage equilibria) is calculated, and the individual is assigned to the population for which its genotype probability is highest. We used the likelihood method of Rannala and Mountain (1997), implemented in the software gsi_sim[7] (Anderson et al., 2008), to compute the genotype prob-

[5] Belkhir, K., P. Borsa, L. Chikhi, N. Raufaste, and F. Bonhomme. 1996–2004. GENETIX 4.05, logiciel sous WindowsTM pour le génétique des populations. Laboratoire Génome, Populations, Interactions, CNRS UMR 5000, Université de Montpellier II, Montpellier, France. [Available from http://kimura.univ-montp2.fr/genetix.]

[6] Felsenstein, J. 2005. PHYLIP (Phylogeny Inference Package), vers. 3.6. Department of Genome Sciences, Univ.Washington, Seattle. [Available from http://evolution.genetics.washington.edu/phylip.html.]

[7] Available from http://swfsc.noaa.gov/textblock.aspx?Division=FED&ParentMenuID=54&id=12964.

Table 2

List of the 96 single nucleotide polymorphism (SNP) loci used to construct the baseline for genetic stock identification of Chinook Salmon (*Oncorhynchus tshawytscha*) from the west coast of North America, with dbSNP accession numbers (from the National Center for Biotechnology Information online repository for short genetic variations; https://www.ncbi.nlm.nih.gov/snp) and source reference (S_R) where available: 1=Clemento et al., 2011; 2=Smith et al., 2005a; 3=Campbell and Narum, 2008; 4=Smith et al., 2005b.

Locus	dbSNP	S_R	Locus	dbSNP	S_R	Locus	dbSNP	S_R
Ots_94857-232	ss275518685	1	Ots_110495-380	ss275518741	1	Ots_131906-141	ss275518787	1
Ots_96222-525	ss275518688	1	Ots_110551-64	ss275518742	1	Ots_AldB1-122	ss275518788	1
Ots_96500-180	ss275518689	1	OkiOts_120255-113	unpubl.	–	Ots_AldoB4-183	ss275518789	1
Ots_97077-179	ss275518691	1	Ots_111312-435	ss275518746	1	Ots_Myc-366	ss275518795	1
Ots_99550-204	ss275518695	1	Ots_111666-408	ss275518747	1	Ots_ALDBINT1-SNP1	ss275518796	1
Ots_100884-287	ss275518696	1	Ots_111681-657	ss275518748	1	Ots_NAML12-SNP1	ss275518798	1
Ots_101119-381	ss275518697	1	Ots_112208-722	ss275518749	1	Ots_ARNT-195	unpubl.	–
Ots_101704-143	ss275518699	1	Ots_112301-43	ss275518750	1	Ots_RAG3	unpubl.	–
Ots_102213-210	ss275518702	1	Ots_112419-131	ss275518751	1	Ots AsnRS-60	ss48398657	2
Ots_102414-395	ss275518703	1	Ots_112820-284	ss275518752	1	Ots_aspat-196	ss65917744	3
Ots_102420-494	ss275518704	1	Ots_112876-371	ss275518753	1	Ots_CD59-2	unpubl.	–
Ots_102457-132	ss275518705	1	Ots_113242-216	ss275518754	1	Ots_CD63	unpubl.	–
Ots_102801-308	ss275518706	1	Ots_113457-40	ss275518755	1	Ots_EP-529	unpubl.	–
Ots_102867-609	ss275518707	1	Ots_117043-255	ss275518757	1	Ots_GDH-81x	ss65917741	3
Ots_103041-52	ss275518708	1	Ots_117242-136	ss275518759	1	Ots_HSP90B-385	ss65713207	2
Ots_104063-132	ss275518711	1	Ots_117432-409	ss275518762	1	Ots_MHC1	ss49851328	4
Ots_104569-86	ss275518714	1	Ots_118175-479	ss275518763	1	Ots_mybp-85	unpubl.	–
Ots_105105-613	ss275518715	1	Ots_118205-61	ss275518764	1	Ots_myoD-364	ss65917726	3
Ots_105132-200	ss275518716	1	Ots_118938-325	ss275518765	1	Ots_Ots311-101x	ss65917748	3
Ots_105401-325	ss275518718	1	Ots_122414-56	ss275518767	1	Ots_PGK-54	unpubl.	–
Ots_105407-117	ss275518719	1	Ots_123048-521	ss275518768	1	Ots_Prl2	ss49851322	4
Ots_106499-70	ss275518724	1	Ots_123921-111	ss275518770	1	Ots_RFC2-558	ss48398670	2
Ots_106747-239	ss275518725	1	Ots_124774-477	ss275518771	1	Ots_SClkF2R2-135	ss48398694	2
Ots_107074-284	ss275518726	1	Ots_127236-62	ss275518773	1	Ots_SWS1op-182	ss48398635	2
Ots_107285-93	ss275518728	1	Ots_128302-57	ss275518775	1	Ots TAPBP	unpubl.	–
Ots_107806-821	ss275518730	1	Ots_128693-461	ss275518777	1	Ots_u07-07.161	unpubl.	–
Ots_108007-208	ss275518731	1	Ots_128757-61	ss275518778	1	Ots_u07-49.290	unpubl.	–
Ots_108390-329	ss275518732	1	Ots_129144-472	ss275518779	1	Ots_u4-92	ss48398636	2
Ots_108735-302	ss275518733	1	Ots 129170-683	ss275518780	1	Ots_BMP2-SNP1	ss275518800	1
Ots_109693-392	ss275518737	1	Ots_129458-451	ss275518782	1	Ots_TF1-SNP1	ss275518802	1
Ots_110064-383	ss275518738	1	Ots_130720-99	ss275518784	1	Ots_S71-336	unpubl.	–
Ots_110201-363	ss275518739	1	Ots_131460-584	ss275518785	1	Ots_unk_526	unpubl.	–

abilities, employing a leave-one-out procedure that excludes the gene copies of the individual being assigned and recalculates population allele frequencies before assignment. Analogous to the THL procedure of Anderson (2010), both the training and holdout sets were included for estimation of population allele frequencies. However, assignments of individuals in the training set were excluded from the results to avoid any high-grading bias of assignment accuracy (Anderson, 2010).

Analysis of simulated mixed fisheries is a common method for evaluation of the resolving power of a baseline for stock identification (Fournier et al., 1984; Wood et al., 1987; Kalinowski, 2004; Beacham et al., 2006). In many studies, samples from simulated fisheries that consist entirely of fish from one population are analyzed in so called "100% simulations." However, such simulations typically do not assess how well the baseline will perform on samples from fisheries that exploit more than one stock. Therefore, we conducted simulations with 20 different mixing proportion vectors. The population composition of these mixtures was determined by using the baseline to estimate the relative proportions of reporting units present in 20 different month-by-area strata sampled from commercial fisheries off the coast of California and Oregon in 2010 and 2011 (E. Crandall et al., unpubl. data).

These vectors reflect mixing proportions that are expected to be encountered in PFMC fisheries. For a given value of the mixing proportion vector of all populations, a replicate simulation consisted of 1) simulating the number of fish from each population in a sample size of 200 by drawing a multinomial random variable with cell probabilities equal to the mixing proportion vector; 2) simulating the genotypes of

the individuals from each population in the mixture sample with 2 different techniques ("cross-validation over gene copies" [CV-GC] and K-fold cross validation [K-fold], see next paragraph); 3) calculating the maximum likelihood estimator (MLE) of the mixture proportions for all the populations from the simulated sample through use of the baseline, which contains all training and holdout individuals; and 4) estimating the mixing proportion of each reporting unit by summing the mixing proportion estimates of its constituent populations. For each of the 20 values of the mixing proportion vectors, 20,000 replicates were conducted with CV-GC, and 1000 replicates were conducted with K-fold. For both methods, the 5% and 95% quantiles of the distribution of the MLE of reporting-unit proportions were calculated from the replicates for each mixing proportion vector.

Simulations were undertaken in 2 different ways. With CV-GC, genotypes were simulated by randomly sampling gene copies from the holdout set (to avoid high-grading bias), and those same gene copies were removed from the baseline when calculating the likelihood of population origin for the simulated individual (see Anderson et al., 2008). With K-fold, genotypes were simulated by drawing entire individuals without replacement (a technique commonly referred to as "jackknifing") from the holdout set to form the mixture sample. Those sampled individuals were not included in the baseline, but all unsampled individuals from the holdout set were included in the baseline for estimation of the mixing proportions.

Mixed fishery samples

Samples from 2090 salmon landed in fisheries in 2010 were collected by the California Department of Fish and Game (now Wildlife) at California ports. Just over half of these fish carried CWTs that identified their population of origin. All samples were genotyped with our panel of 96 loci. Individuals successfully genotyped at fewer than 60 loci were removed from further analysis. Failed genotypes were ones that either clustered with negative controls during scoring or fell outside of defined heterozygote and homozygote clusters, likely indicating sample contamination (Smith et al., 2011; Larson et al., 2013). We also used an individual heterozygosity (iHz; the proportion of heterozygous loci for each fish) criterion of iHz >0.56 to identify and exclude potentially contaminated samples. Simulations of contaminated genotypes determined by using observed allele frequencies, indicated little overlap in the distribution of iHz for contaminated and uncontaminated samples (data not shown) and that uncontaminated samples rarely had iHz >0.56.

We used the maximum likelihood framework in gsi_sim to estimate the mixing proportion of different populations among the 2090 fish, and then used that MLE as the prior for calculation of the posterior probability of population of origin for each fish. Posterior probabilities of origination from different reporting units were obtained through summation of the population-specific probabilities over all populations in a reporting unit. Individuals were then assigned to the reporting unit with the highest posterior probability.

Because all fish would be assigned to a maximum a posteriori (MAP) population regardless of true origin, we employed a simulation method similar to that in Cornuet et al. (1999), but which was modified to account for missing data, to detect fish that might have originated from a population that was not in the baseline or that had an otherwise aberrant genotype. Briefly, for each fish from the fishery assigned to a population, the allele frequencies from the MAP population were used to simulate 10,000 genotypes with an identical pattern of missing data (if any) to that of the fish that was assigned.

The log-probability of each simulated genotype was computed, given that it came from the population it was simulated from, and then the distribution of those values was compared with the log-probability, L_a, of the actual assigned fish's genotype, given the allele frequencies in the MAP population, on the basis of a z-score (L_a minus the mean of the simulated values, all divided by the standard deviation of the simulated values). The z-score calculation was done conditional on the exact pattern of missing data and was implemented in the C programming language as part of the gsi_sim software. A low-confidence assignment was defined to be one that had a z-score <3.0 and had either a reporting unit posterior probability <0.9 or had fewer than 90 loci successfully genotyped. Fish with low confidence assignments were left in an "unassigned" category.

Results

Genotyping and basic population genetics

We successfully genotyped 8031 samples from 69 populations for the baseline and submitted the data to the Dryad Digital Repository (http://doi.org/10.5061/dryad.5745sv). All individuals were retained in the baseline, regardless of missing data because we desired a realistic representation of missing data patterns for subsequent power analyses. One locus failed to amplify entirely in the Copper River population, and 3 loci failed in the Coho Salmon sample. Unbiased estimates of heterozygosity (Nei, 1978) ranged from 0.194 in the Rapid River Hatchery stock of the Snake River reporting unit to 0.381 in the Smith River population. The Coho Salmon in the baseline had very low heterozygosity (0.094). Observed heterozygosity and mean number of alleles generally were lower for populations from north of the Columbia River (Table 1), likely due to an ascertainment bias resulting from the selection of SNPs with high MAFs in California and Oregon populations.

Significant deviations from HWE ($P<0.0001$) were observed at various loci in 17 populations but represented <0.3% of all observations. Only the Butte Creek spring-run, Trinity River Hatchery spring-run, and Smith River populations were not in HWE at more than 2 loci, with 5, 5, and 4 significant tests, respectively. Similarly, only 3 loci deviated from HWE in more than 2 populations: Ots_u07_07.161 in 3 populations, Ots_111312-435 in 6 populations, and Ots_111666-408 in 4 populations. Only 1 population (Trinity River Hatchery spring run) displayed significant LD ($P<0.001$) at more than 1% of locus comparisons (1.14%), and, over all populations, the percentage of significant comparisons was 0.16%. Only 2 locus pairs were significant in more than 5 populations: Ots_AldB1-122 and Ots_AldoB4-183, known to be in the same gene complex, were in LD in 42 populations, and Ots_Myc-366 and Ots_unk-526 displayed LD in 8 populations.

A large range in the degree of differentiation between populations was observed (Table 1). Mean F_{ST} across all populations (excluding Coho Salmon) was 0.183, indicating that approximately 18% of genetic variation was partitioned between population samples. Within reporting units that contained more than one population (N=18), pairwise F_{ST} was between 0.000 and 0.152 and had a mean value of 0.018. Ten pairwise comparisons, all within reporting units, were not significantly different from zero ($P<0.01$). Between reporting units, F_{ST} values ranged from 0.005 to 0.411 and had a mean value of 0.188. The least differentiated populations were the fall-run populations from California's Central Valley, as has been observed with other genetic data sets (Williamson and May, 2005; Seeb et al., 2007).

Genetic structure of the Chinook Salmon populations in the baseline is displayed in an unrooted neighbor-joining dendrogram (Fig. 1). Relationships are in strong agreement with expectations that were based on geography and previous studies (Waples et al., 2004; Beacham et al., 2006; Templin et al., 2011; Moran et al., 2013); populations generally are organized north to south along the main branch, and populations from within the same drainage usually cluster together.

Populations from California's Central Valley are monophyletic in relation to the remainder of the populations but are characterized by short branch lengths, small distances between nodes, and low bootstrap support. Central Valley spring-run and fall-run populations also are monophyletic, with the exception of the Feather River Hatchery spring run, which is included in the fall-run reporting unit because of a history of substantial introgression between the runs and the consequent difficulty of genetically distinguishing this stock from fall-run fish (Garza et al.[8]). Sacramento River winter-run fish are quite distinct as a result of a well-documented recent bottleneck (Hedrick et al., 1995) and have one of the longest branches on the tree, with bootstrap support of 100%. Fish from rivers in northern California and coastal Oregon also form a monophyletic group. Columbia River populations are dispersed throughout the tree, although populations from the same reporting unit generally share a common branch, as do populations from Alaska.

Accuracy of assignment and mixture estimations

The 7669 individuals that remained after removal of training-set fish were subjected to self-assignment with gsi_sim (Table 1). Correct assignment to population ranged from 13% for the Butte Creek fall-run population to 100% for 5 different populations. The following reporting units had the lowest correct assignment rates to population: Central Valley fall run, Upper Columbia River summer/fall run, and Western Alaska, Lower Kuskokwim River, averaging 28%, 36%, and 40%, respectively. The lowest rate of correct assignment to reporting unit was for the Siuslaw River population from the Mid Oregon Coast reporting unit, with over half of the individuals assigning to populations in the North Oregon coast reporting unit. The largest change in correct assignment percentage from population to reporting unit was for the Central Valley fall run, which increased to 91%.

The results of the mixture simulations for the 9 reporting units most frequently found in California and Oregon fisheries appear in Figure 2. Results for the remaining reporting units are not shown because they are relatively uninformative as a result of the rarity with which populations from north of the Columbia River are encountered at the southern end of the California Current marine ecosystem, an observation corroborated by historical CWT data: in the 3 decades since 1983, only 0.5% of all CWTs recovered from Chinook Salmon in California ocean fisheries were from stocks outside of California or Oregon (Regional Mark Information System, Regional Mark Processing Center, http://www.rmpc.org). Accurate estimates of the mixing proportions were obtained for fishery samples simulated either by CV-GC or by K-fold. The mean maximum likelihood estimate of the proportion of each reporting unit was generally highly correlated with the true proportion, indicating that any bias was very small.

For 6 reporting units (Central Valley fall run, Sacramento River winter run, Klamath River, California Coast, Rogue River, and North Oregon Coast), the 5% and 95% quantiles for reporting-unit mixing proportions corresponded closely with the quantiles one would obtain with perfect identification of all fish (see the gray regions in Fig. 2). The somewhat wider GSI quan-

[8] Garza, J. C., S. M. Blankenship, C. Lemaire, and G. Charrier. 2008. Genetic population structure of Chinook Salmon (*Oncorhynchus tshawytscha*) in California's Central Valley. Final report for CalFed project "Comprehensive evaluation of population structure and diversity for Central Valley Salmon," 54 p. [Available from http://swfsc.noaa.gov/publications/FED/01110.pdf.]

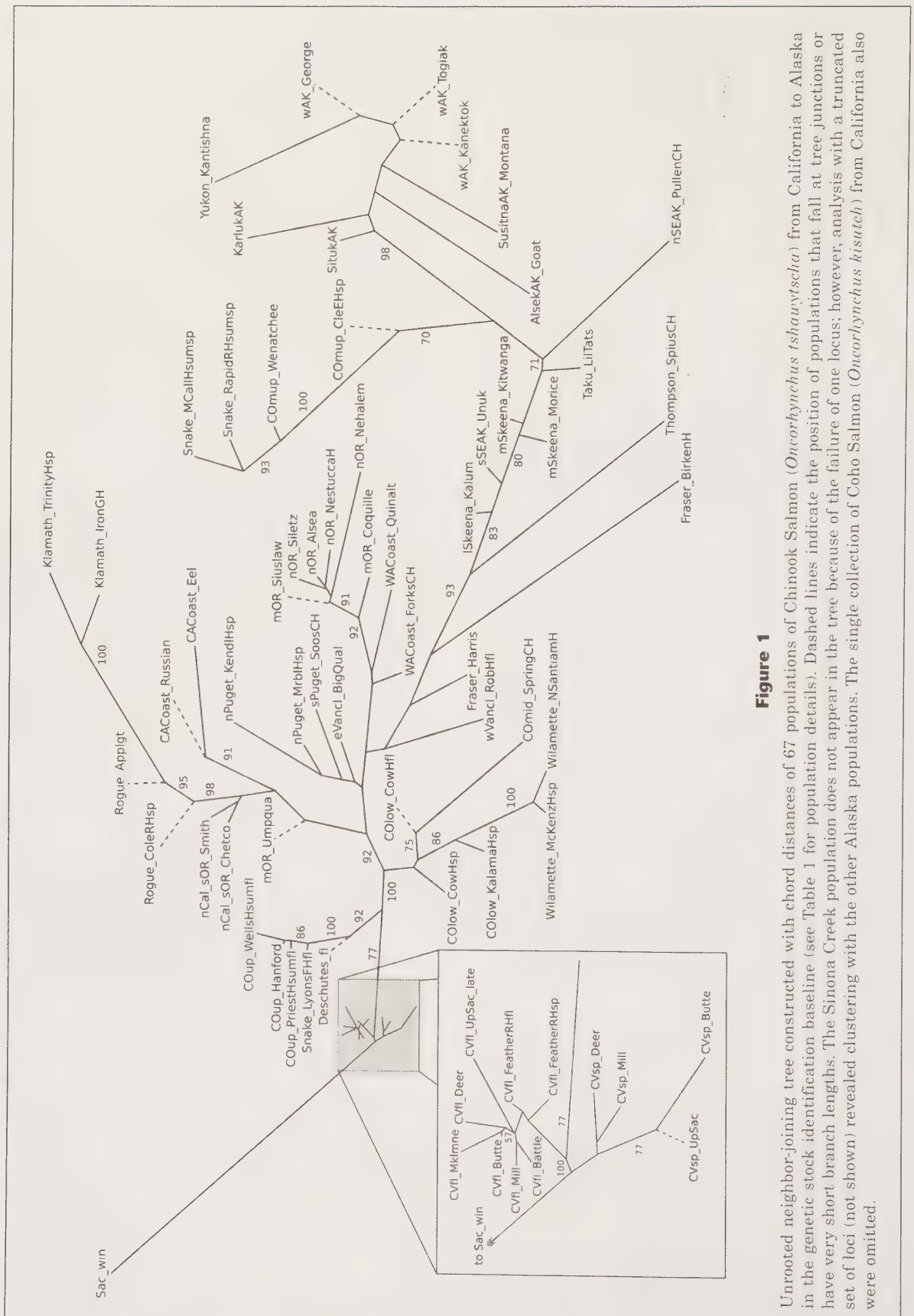

Figure 1

Unrooted neighbor-joining tree constructed with chord distances of 67 populations of Chinook Salmon (*Oncorhynchus tshawytscha*) from California to Alaska in the genetic stock identification baseline (see Table 1 for population details). Dashed lines indicate the position of populations that fall at tree junctions or have very short branch lengths. The Sinona Creek population does not appear in the tree because of the failure of one locus; however, analysis with a truncated set of loci (not shown) revealed clustering with the other Alaska populations. The single collection of Coho Salmon (*Oncorhynchus kisutch*) from California also were omitted.

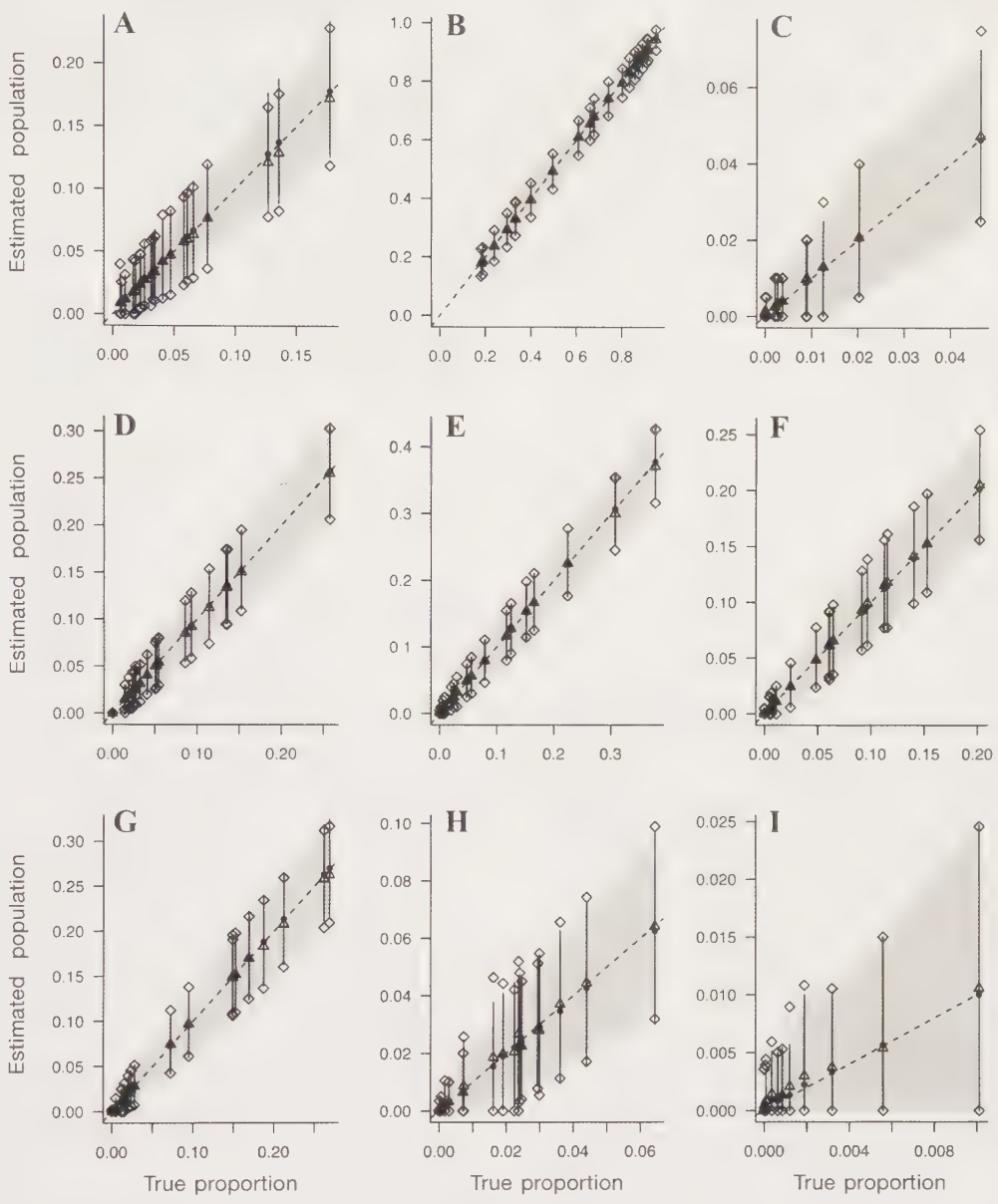

Figure 2

Estimates of mixing proportions from cross-validation over gene copies (CV-GC) and K-fold simulations for the 9 most abundant reporting units of Chinook Salmon (*Oncorhynchus tshawytscha*) encountered in California fisheries: Central Valley (**A**) spring, (**B**) fall, and (**C**) winter; (**D**) California Coast; (**E**) Klamath River; (**F**) North California/South Oregon Coast; (**G**) Rogue River; and (**H**) Mid Oregon Coast; and (**I**) North Oregon Coast. The x-axis gives the true proportion of fish from each reporting unit, and the y-axis gives the estimated proportion. The dashed line is the $y=x$ line. Gray shaded regions give the range between the 5% and 95% quantiles of estimates that would be achieved with perfect assignment of fish to a reporting unit (i.e., they represent the uncertainty due to the fact that fishery proportions are estimated with a finite sample; in our simulations, a sample of 200 fish). The 5% and 95% quantiles of the estimates derived from the CV-GC and the K-fold replicates are shown with vertical line segments and open diamonds, respectively. Reporting units for which these bars and diamonds coincide with the gray region had estimated proportions as accurate as one would expect given unambiguous identification of fish to reporting unit. Filled circles and open triangles indicate the mean over 20,000 CV-GC and 1000 K-fold replicates, respectively. These points fall along the dotted line when the estimator is unbiased.

Table 3

Genetic stock identification (GSI) results from assignment of samples of Chinook Salmon (*Oncorhynchus tshawytscha*) collected in 2010 from the California fishery to their source populations through the use of a single nucleotide polymorphism baseline, as well as concordance with recoveries of coded wire tags (CWTs). N.=North; S.=South.

Stock	Number from GSI	Number with CWT	Number of GSI~CWT matches	GSI~CWT agreement (%)
California Coast	30	1	0	0.00%
Central Valley fall	1581	958	957	99.90%
Central Valley spring	7	1	0	0.00%
Klamath River	108	50	49	98.00%
Lower Columbia spring	1	0	0	–
Mid Columbia Tule fall	7	2	2	100.00%
Mid Oregon Coast	14	1	0	0.00%
N. California/S. Oregon Coast	58	25	25	100.00%
Rogue River	154	11	5	45.45%
Snake River fall	1	1	1	100.00%
Upper Columbia summer/fall	8	2	2	100.00%
Total	1969	1052	1041	98.95%

tile intervals observed for the Central Valley spring-run reporting unit were likely due to its similarity to the Central Valley fall-run reporting unit, combined with the fact that the spring run is typically at much lower abundance than is the fall run. Likewise, the genetic similarity of fish from the Mid Oregon Coast reporting unit and the Northern California/Southern Oregon Coast reporting unit made it difficult to accurately estimate mixing proportions for these reporting units; however, the estimates were still quite good and largely unbiased. Therefore, despite the enlarged quantile intervals for Central Valley spring-run and the Mid Oregon Coast reporting units versus Northern California–Southern Oregon reporting unit, the results from both simulation methods indicated that the SNP baseline is capable of providing estimates of the true mixing proportions for most reporting units that are nearly as accurate as one would expect given perfect identification of each fish.

Fishery samples

Of the 2090 samples collected from California fisheries in 2010, 85 samples were excluded because they did not yield acceptable genotypes (<60 successfully genotyped loci) and 2 samples were excluded because they were duplicates of 2 other samples in the data set. Eight fish exceeded the iHz threshold of 0.56 and were removed because of potential contamination. Seven fish were identified as Coho Salmon through both GSI assignment and with the species-diagnostic assay. Another 18 samples did not meet assignment confidence criteria (mean z-score of –3.99 and a mean of 75 successfully genotyped loci) and were also excluded. For the remaining 1969 fish, assignment probabilities to reporting unit ranged from 36.4% to 100% (mean 98.5%) and z-scores ranged from –4.12 to 2.68 (mean –0.04). Central Valley fall-run fish dominated the stock composition, accounting for more than 80% of sampled fish, followed by the Rogue River (7.79%) and Klamath River (5.46%) reporting units and 8 other stocks with <5% (Table 3). Of the assigned fish, 1052 retained CWTs that were recovered. Genetic assignment to reporting unit disagreed with CWT origin for only 11 fish (1.05%), and, of these mismatches, 6 were fish with Klamath or Smith River tags that were assigned to the genetically similar Rogue River reporting unit.

Discussion

Here we describe one of the first large-scale SNP baselines for genetic stock identification of Chinook Salmon and the first designed for use with fisheries in the California Current large marine ecosystem off the contiguous United States. Chinook Salmon are an economically and ecologically important species and are a major component of fisheries in the North Pacific Ocean. We genotyped more than 8000 individual fish from 69 distinct populations at 96 SNP loci to construct the baseline. The reporting units included in the baseline represent the likely sources for more than 99% of the fish typically encountered in PFMC fisheries off California and Oregon.

Furthermore, results from mixture analyses and self-assignment indicate that the baseline has near maximum possible power for discrimination of Chinook Salmon stocks at the reporting unit level. Estimates of

the mixture proportions of Central Valley fall, Central Valley winter, California Coast, Klamath River, and Rogue River reporting units (Fig. 2) were no more variable than were estimates that would have been obtained if every fish had carried an unambiguous reporting-unit tag. Estimates of mixing proportions for Central Valley spring, North California/South Oregon, and Mid Oregon Coast reporting units were somewhat more variable but appeared to be nearly unbiased. In the ocean fishery sample, assignments of more than 1000 individuals to reporting unit, determined with our baseline, were highly concordant (98.95%) with the CWTs recovered from the same fish. This SNP baseline, therefore, represents an important addition to the technologies available to managers and researchers.

Methodological considerations

Management of salmon fisheries in the Pacific Ocean off North America can be roughly divided into 3 fisheries by region: California and Oregon fisheries, managed by the Pacific Fishery Management Council (PFMC); Washington, British Columbia, Canada, and southeastern Alaska fisheries, subject to the international Pacific Salmon Treaty, reporting to and regulated by the Pacific Salmon Commission; and fisheries farther north and west in Alaska that are managed by the state, with salmon bycatch under the purview of the North Pacific Fishery Management Council. The genetic baseline described here was designed primarily to identify fish caught in PFMC ocean fisheries and in ecological investigations in the southern portion of the California Current ecosystem and its associated tributary rivers and streams. We have shown that it performs well in this area but, because of an ascertainment strategy during SNP discovery that included individuals from the Columbia River and British Columbia (Clemento et al., 2011), the baseline also has sufficient statistical power to identify the source of some fish from elsewhere in the North American range of this species.

We observed high rates of self-assignment to reporting unit for all regions represented in the baseline, although some reporting units clearly were composed of populations with minimal differentiation from each other. Moreover, the utility of our baseline could be extended effectively by simply genotyping the same panel of SNPs on additional populations in those regions, despite the reduced heterozygosity and mean number of alleles (Table 1), and presumably statistical power in our baseline, for populations from Canada and Alaska.

Other SNP baselines for Chinook Salmon also have been described or are being constructed. Templin et al. (2011) described a 45 SNP locus baseline for populations in the northern and western parts of the Chinook Salmon range, designed primarily for GSI of populations from western and southcentral Alaska. This same baseline was used also to probe the seasonal distribution and migration pattern of Chinook Salmon in the Bering Sea and North Pacific Ocean (Larson et al., 2013). Despite the presence of 14 populations from California, Oregon, and Washington in that baseline, Larson et al. (2013) appropriately emphasized that resolution of those southern populations is sufficient only for broad-scale assignments. Similarly, Warheit et al.[3] described the marker selection for eventual development of a SNP baseline for application to fisheries managed by the Pacific Salmon Commission.

Although the existence of multiple regional baselines is likely to expand, it still will benefit the entire community of fishery managers and scientists to carefully design marker panels with as much overlap as possible. It is conceivable that 2 or 3 panels of 96 SNPs could provide the level of resolution needed for identification throughout the range of Chinook Salmon. Alternatively, as next-generation sequencing techniques mature, genotyping-by-sequencing (GBS) approaches might yield data for GSI at a lower cost than that with current genotyping techniques. A GBS approach could be used to simultaneously genotype all of the SNPs in each of the regional baselines, allowing mixed-stock analysis throughout the range of this species.

Inclusion of the species-diagnostic marker and Coho Salmon sample in the baseline provided insight into the prevalence of misidentification of Coho Salmon in ocean fisheries. In the 2010 fishery off California, 7 fish sampled as Chinook Salmon were found to be Coho Salmon. Without methods to identify Coho Salmon, the baseline would assign them with erroneously high confidence to a northern, low-heterozygosity Chinook Salmon population (data not shown). This problem is characteristic of most statistical methods for performing GSI: if an individual's true population of origin is *not* included in the baseline, then even if *all* the populations in the baseline are very poor candidates for that fish's origin, that fish might still be assigned with high posterior probability to one of the populations. This situation occurs when one population is much more likely to be the population of origin, than any of the other incorrect populations, even if it is not a likely origin for that individual on an absolute scale.

We introduced a simulation-based z-score method, implemented in gsi_sim, to identify fish that likely have not originated from populations in the baseline. An alternative, Bayesian nonparametric approach to dealing with fish from populations not in the baseline identifies those fish and estimates the allele frequencies in their (unrepresented) source population (Pella and Masuda, 2000). That approach is appropriate particularly when large numbers of fish are sampled from each of the populations that are not included in the baseline and when the unrepresented populations are quite divergent from all of the populations in the baseline.

We chose the *z*-score approach over the Bayesian nonparametric approach for 3 main reasons: 1) it is computationally fast and simple (there are no convergence problems that might be difficult to detect); 2) our baseline was sufficiently comprehensive for stocks that

contribute to PFMC fisheries, and therefore it was unlikely that large numbers of fish would originate from any single unrepresented population, let alone a highly divergent one; and 3) our approach is more appropriate for identification of fish whose genotypes are aberrant because of genotyping complications or sample contamination. Regardless of which method is used, all GSI estimation should include some analysis to identify fish that are either from populations not included in the baseline or that have aberrant genotypes for another reason.

GSI is highly dependent on source populations being genetically differentiated enough from one another for discrimination. In situations where hatchery broodstock transfers, supplementation, or other processes increase straying and gene flow between fish populations, genetic differentiation decreases and it can become more difficult to use GSI. Such is the case in the Central Valley of California, where average F_{ST} between populations in the fall-run reporting unit was 0.006 and in the spring-run reporting unit was 0.013. In the dendrogram (Fig. 1), this region was characterized by extremely short branch lengths, small internodal differences, and weak bootstrap support. Extensive straying of hatchery salmon due to off-site juvenile releases (California Hatchery Scientific Review Group [9]) and water operations (Fisher, 1994) has eliminated historical differentiation between populations of fall-run Chinook Salmon (Williamson and May, 2005). Introgression between fall-run and spring-run fish at the Feather River Hatchery, and likely elsewhere within the basin, has reduced differentiation between these 2 phenotypes, with mean F_{ST} of 0.025 between fall-run and naturally spawning spring-run populations.

Sampling of different stocks for baseline construction in the presence of high stray rates is not entirely straightforward, particularly when populations are largely sympatric and not visually distinguishable. For example, there is clearly a single fish from the Central Valley fall-run reporting unit that was sampled as a winter-run fish in our baseline. These types of occurrences are almost inevitable given the high degree of disturbance and hatchery supplementation over much of the range of Chinook Salmon. One approach is to move fish with discrepant genotypes from the baseline populations in which they were sampled to the ones to which they are assigned with GSI (e.g., Banks et al., 2000). However, such a procedure can introduce an upward bias in the predicted accuracy of the baseline, if, in fact, the removed fish actually do belong to the populations from which they were sampled and simply have unlikely genotypes at the genetic markers used for baseline construction. We chose to be conservative by both 1) accepting a slightly lower rate of predicted resolution obtained by not removing miscategorized fish and 2) avoiding an upward bias in predicted GSI accuracy if the fish removed are not miscategorized.

[9] California Hatchery Scientific Review Group. 2012. California Hatchery Review Report, 102 p. Prepared for the U.S. Fish and Wildlife Service and Pacific States Marine Faisheries Commission. [Available from http://swfsc.noaa.gov/publications/FED/01067.pdf and (appendices) http://cahatcheryreview.com/reports.]

Implications for management

Accurately estimating the proportion of fish from different populations in mixed-stock ocean fisheries has important applications for harvest management and conservation. Stocks that comingle in ocean fisheries can vary widely in productivity and abundance. Without precise information on their ocean distribution, as can be provided by GSI, managers have few options for protection of depressed or at-risk stocks from fishery impacts other than that of shutting down or curtailing fisheries over broad areas, as is currently done (Beacham et al., 2008). For example, in 2008 and 2009, the largest closures on record of fisheries in California and Oregon were enacted to protect the severely reduced Central Valley fall-run stock (Lindley et al., 2009). The economic effects of fishery closures are substantial, resulting in millions of dollars of lost income for fishermen, coastal communities, and retailers (Michael [10]).

Management of Chinook Salmon in California, Oregon, and Washington and in fisheries managed by the Pacific Salmon Commission depends heavily on information generated by an elaborate CWT program (Hankin et al., 2005). Tiny wire tags are mechanically implanted into the heads of juvenile fish, with each tag bearing a code that identifies the release group and source hatchery (or stock) of that fish. Tagging of naturally spawned juvenile fish has generally proven unsuccessful (Beacham et al., 1996), and, for that reason, tagged hatchery stocks are used as proxies to estimate fishery impacts for groups of natural stocks. Aside from the largely unvalidated assumption that such proxies accurately reflect fishery impacts on associated natural stocks (Hankin et al., 2005), the physical effects of tagging fish and removing their nerve-rich adipose fin (Buckland-Nicks et al., 2012) as an associated external mark can increase disease transmission (Elliott and Pascho, 2001), interfere with homing (Morrison and Zajac, 1987; Habicht et al., 1998) and swimming ability (Reimchen and Temple, 2004) and may affect size-at-return for adult salmon (Vander Haegen et al., 2005). Moreover, extremely low recovery rates mean that CWT data are often quite limited and great uncertainty is frequently associated with the estimates derived from them (Hankin et al., 2005).

GSI has been advanced as an alternative to CWTs in fishery management for several decades. Our direct

[10] Michael, J. 2010. Employment impacts of California salmon fishery closures in 2008 and 2009. Business Forecasting Center, Univ. of the Pacific, Stockton, CA. [Available from http://forecast.pacific.edu/BFC%20salmon%20jobs.pdf.]

comparison of CWT with genetic assignments demonstrates that our baseline is capable of identifying fish to reporting unit with accuracy comparable to that of CWTs. Furthermore, the use of GSI can identify considerably more fish to reporting unit, including fish from natural stocks. Confident genetic assignments were obtained for ~94% of fish from the 2010 fishery sample, but only 1052 of those fish carried CWTs and this number is inflated partially because of oversampling of fish believed to carry CWTs.

Fishery management decisions rely heavily on cohort-based ocean harvest models (cf., O'Farrell et al., 2012), which require information on both stock of origin and age of fish impacted by fisheries. Because GSI does not provide the age of individuals, it is not by itself an adequate alternative to CWTs. Nonetheless, new statistical methods capable of integrating GSI, length data, and scale- or otolith-based age data have been developed recently, allowing managers to draw important inference about PFMC fisheries that are not possible with CWTs alone (Satterthwaite et al., 2014). Moreover, pedigree-based genetic tagging *does* supply age for salmon (Anderson and Garza, 2006; Garza and Anderson[2]). This method, termed "parentage-based tagging" (PBT), can identify the actual parents of a genotyped individual through parentage analysis if they have been genotyped with the same genetic markers. If the parents' date of spawning is known, as it typically is in a hatchery, then the reconstructed pedigrees yield the offspring's precise age and any associated parental spawning information.

Importantly, both PBT and GSI can be undertaken with the same SNP genotypes, and the SNPs used in our GSI baseline are sufficiently powerful for PBT with Chinook Salmon from California to Washington (Anderson, 2012). This interoperability of genotype data enables an integrated program that uses both GSI and PBT simultaneously, providing identification for all fish in a fishery or ecological sample and yielding significantly greater inference than either method alone. For example, GSI cannot distinguish between spring-run and fall-run fish from the Feather River Hatchery in California, but PBT distinguishes them, almost without error, from any mixture. Likewise, although it is difficult to implement PBT in natural populations, the same SNP genotypes used in a PBT analysis permit accurate identification (by GSI) of fish from the naturally spawning, ESA-listed "California Coastal Chinook Salmon Evolutionarily Significant Unit."

Conclusions

The advent of high-throughput SNP genotyping already has revolutionized human genetics (Jenkins and Gibson, 2002), providing previously unattainable resolution (e.g., Novembre et al., 2008) and is poised to do the same for fisheries biology and management. As described here, we used a careful and statistically valid power analysis of SNP genotypes from a large number of Chinook Salmon populations concentrated at the southern end of the native range of this species to show that SNPs can provide a powerful baseline for genetic stock identification (see also Larson et al., 2013) in fisheries and ecological investigation in the California Current large marine ecosystem and its tributaries in California and Oregon. We predict that these advances in genetic resources and methods will foster fundamental improvements in the way salmon populations are studied, monitored, and managed.

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Effect of demography on spatial distribution: movement patterns of the Albemarle Sound–Roanoke River stock of Striped Bass (*Morone saxatilis*) in relation to their recovery

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Abstract—We analyzed tag returns from a long-term tagging program to evaluate the movement patterns of the Albemarle Sound–Roanoke River (AR) stock of Striped Bass (*Morone saxatilis*) during a period of stock recovery in 1991–2008. The AR stock was found to increase its movement outside the Albemarle Sound estuary (from <4% to 15–31%) as it recovered from 1991 to 2008. Analysis with multinomial logistic regression where recapture area was modeled as a function of fish size and stock abundance indicated that Striped Bass from the AR stock exhibit a strong size-dependent emigration pattern. Larger (older) adults >600 mm in total length (TL) were much more likely to emigrate to ocean habitats (after spawning) than were smaller adults (350–600 mm TL), which mostly remained in inshore estuarine habitats. Smaller adults showed evidence of density-dependent movement and were recaptured only in adjacent estuarine systems, the Pamlico Sound and lower Chesapeake Bay, during periods of increased stock abundance. Assessment and management strategies for the AR stock of Striped Bass could be improved by accounting for movement (and hence harvest) outside the currently assumed stock boundary. More broadly, this study illustrates that changes in the demographics, such as size structure and total abundance, within fish populations can result in major shifts in their distribution and that long-term tagging data are useful in detection of such population-level changes in movement patterns.

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The demographics of fish populations can be important in shaping their movement patterns. Numerous species have been shown to increase their distributional range or movement distances as population abundance increases (Swain and Wade, 1993; Brodie et al., 1998; Overholtz, 2002; Abesamis and Russ, 2005; Dunning et al., 2006), a response presumably due to density-dependent mechanisms (e.g., intraspecific competition for food or the saturation of optimal habitats) (MacCall, 1990). In addition, changes in movement patterns with ontogenetic changes in fish are common because habitat requirements change as species age (Werner and Gilliam, 1984; Dahlgren and Eggleston, 2000).

The demographics of fish populations are continually shifting for reasons that include changes in fishing pressure and the natural environment (e.g., recruitment variation) that can alter age structure and abundance (Longhurst, 2002; Berkeley et al., 2004; Hutchings and Baum, 2005) and in turn cause population-level changes in movement patterns. Understanding if and how population-level movements (and distribution) change over time is of particular importance for exploited fishery species because such changes can pose challenges for assessment and management techniques, for which stock boundaries are often assumed to be static and not dynamic (Winters and Wheeler, 1985; Hammer and Zimmermann, 2005; Link et al., 2011).

Striped Bass (*Morone saxatilis*) occur throughout the East Coast of the United States and have supported important fisheries there for centuries (Merriman, 1941). Tagging studies clearly have shown that spawning populations (or stocks) of Striped Bass in the mid-Atlantic region, which includes the Hudson River, Delaware River, and Chesapeake Bay, generally exhibit an anadromous life-history strategy and undergo extensive seasonal migrations. After spawning in the freshwater portion of their respective estuaries, many adults emigrate to Atlantic

Ocean waters from New Jersey to Maine in early summer, move south in the fall to overwintering habitats in coastal waters from New Jersey to Cape Lookout in North Carolina, then return to their natal estuary in subsequent springs to spawn (Boreman and Lewis, 1987; Waldman et al., 1990; Dorazio et al., 1994; Welsh et al., 2007). In contrast, the Albemarle Sound–Roanoke River (AR) stock of Striped Bass, hereafter referred to as the "AR stock," has historically been viewed as a nonmigratory stock, and most fish are believed to remain in their natal estuarine system, the Albemarle Sound estuary, throughout their lives (Merriman, 1941; Hassler et al.[1]). Indeed, in the most extensive tagging study to date on the AR stock by Hassler et al.[1], virtually all (99%) of the 2428 returns of the 9220 adults tagged in the Roanoke River during the springs of 1959–77, occurred within the Albemarle Sound estuary. The few returns that occurred outside Albemarle Sound (<1% of the total) were from an adjacent estuary (Pamlico Sound); remarkably, no returns were from ocean waters (Hassler et al.[1]).

These differences in migration patterns may have been due to differences in life-history strategies (nonanadromous vs. anadromous) between the AR stock and more northerly stocks, or it could have been a result of a historic lack of larger, older fish (>600 mm in total length [TL]) in the AR stock because of high harvest levels. Differences in life-history strategy would be perplexing given that these stocks occur in the same zoogeographic province (mid-Atlantic coast of the United States) and given that some of them are in close latitudinal proximity (e.g., the AR and Chesapeake Bay stocks). In 1988, the North Carolina Division of Marine Fisheries (NCDMF) began a cooperative tagging program with the North Carolina Wildlife Resources Commission (NCWRC) to address this question and to further investigate the migration dynamics of the AR stock of Striped Bass.

Much of the past work of tagging individuals from the AR stock was done when Striped Bass were at low levels of abundance and overfished (NCDMF and NCWRC[2]). In more recent years (1991–2008), the AR stock, as well as the Chesapeake Bay stock (Richards and Rago, 1999), made a dramatic recovery from their depleted state in the late 1970s and 1980s. The estimated total abundance of the AR stock nearly doubled during the 1990s, increasing from 1.0 to 1.9 million fish, and remained at high levels (>1.8 million fish) throughout the 2000s (NCDMF and NCWRC[2]). In addition, the age and size structure of the stock expanded as larger (>600 mm TL) and older (age 9+) fish became more prevalent as the stock recovered (NCDMF and NCWRC[2]). The recovery of the AR stock was a result of a combination of factors, namely more stringent fishing regulations that increased development to older age classes and improvements in environmental conditions that enhanced spawning habitat and recruitment of young Striped Bass (e.g., regulated river flows that were more conducive for the transport and survival of eggs and larvae) (Rulifson and Manooch, 1990; NCDMF and NCWRC[2]).

For this study, we first addressed the following question: Have Striped Bass of the AR stock increased their movement outside of the Albemarle Sound estuary since population rebuilding in the 1990s? After showing that the movement of the AR stock out of the estuary has indeed increased, we then related recapture locations of tagged individuals to both fish size and total annual stock abundance (density) in an effort to explain this increase in emigration over the past 2 decades (1991–2008). Lastly, we discuss the management implications of this increased movement given the stock is currently considered to be resident.

Materials and methods

Fish tagging

During the springs of 1991–2008, 42,534 adult Striped Bass from the AR stock (mostly >350 mm TL; Fig. 1) were tagged and released on their well-described spawning grounds (Hassler et al.[1]) ~200 km upstream of the mouth of the Roanoke River in North Carolina (Fig. 2A). During weekly sampling events throughout April and May, Striped Bass were collected with an electrofishing boat and transported to a tagging vessel, where they were held in a "live well" until processing. Fish in good condition were measured (TL to the nearest millimeter), weighed (to the nearest gram), and sex was determined by expression of gonadal products. The fish were then tagged just above the posterior tip of the pelvic fin with a Floy (model FM-84[3]) internal anchor tag (Floy Tag, Inc., Seattle, WA). Fish were immediately released after tagging. The streamer of the tags indicated a "reward" (US $5 or a baseball cap) would be offered for reporting information on recaptured Striped Bass (e.g., recovery date and location, and tag number)

[1] Hassler, W. W., N. L. Hill, and J. T. Brown. 1981. The status and abundance of striped bass, Morone saxatilis, in the Roanoke River and Albemarle Sound, North Carolina, 1956–1980. North Carolina Department of Natural Resources and Community Development, Division of Marine Fisheries, Special Scientific Report 38, 156 p. [Available from the Division of Marine Fisheries, 3441 Arendell St., Morehead City, NC 28557.

[2] NCDMF (North Carolina Division of Marine Fisheries) and NCWRC (North Carolina Wildlife Resources Commission). 2013. Amendment I to the North Carolina Estuarine Striped Bass Fishery Management Plan, 420 p + appendices. North Carolina Division of Marine Fisheries, North Carolina Department of Environment and Natural Resources, Morehead City, NC. [Available from http://portal.ncdenr.org/c/document_library/get_file?uuid=d3fdf967-82d5-4653-8b79-20247c5ed5ad&groupId=38337, accessed January 2014.]

[3] Mention of trade names of commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

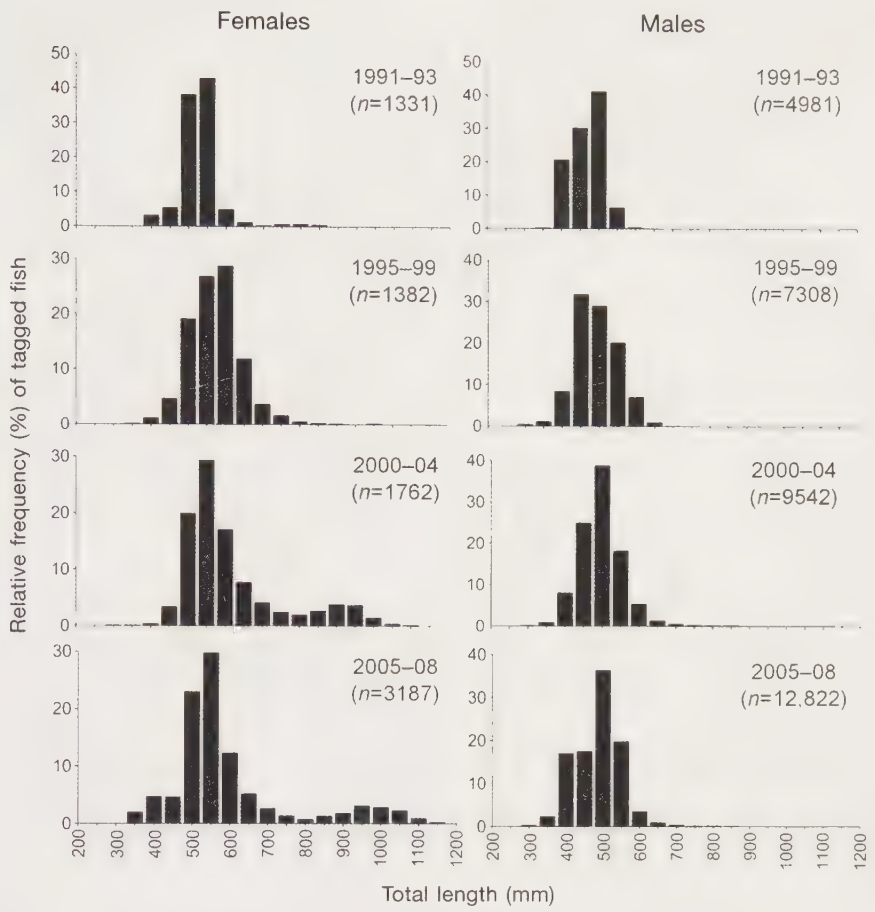

Figure 1

Size distributions of tagged Striped Bass (*Morone saxatilis*) by time period and sex. Fish were collected by electrofishing during spring in the Roanoke River. Note that sex was determined for nearly all (>99%) tagged fish. Data from 1994 were excluded because few fish (n=9) were tagged that year.

to the NCDMF, whose contact information was printed on the tag.

Data analysis

We used multinomial logistic regression to evaluate the effects of fish size and stock abundance on the recapture location (i.e., to evaluate the movements) of Striped Bass of the AR stock. For this analysis, recapture locations of tagged fish were assigned to 1 of 4 broad geographic areas: 1) the Albemarle Sound estuary, 2) the Pamlico Sound estuary, 3) ocean waters of North Carolina, or 4) northern coastal waters from Virginia to Massachusetts (Fig. 2B). Therefore, recapture area constituted a multicategory response variable. Explanatory variables were fish size (TL at tagging) and total annual abundance of the AR stock (1991–2008). Annual abundance estimates (of age 1+ fish) were obtained from a statistical catch-at-age model from the most recent AR stock assessment (NCDMF and NCWRC[2]) and served as a proxy for the annual densities of conspecifics (AR stock only) with which tagged Striped Bass were expected to interact each year. Sex was not included as an explanatory variable because it was confounded with fish size beyond 800 mm TL because all but 4 tag returns from this size range were from females. However, across smaller sizes (400–800 mm TL), over which sexes were more equally represented, similar-size males and females were generally recaptured in the same areas, indicating that movements differed little between sexes.

For the purpose of our analyses, we included only tag returns that occurred after the first 2 weeks but within the first calendar year at liberty. By restricting returns to those returns that occurred within the first calendar year at liberty (on or before 31 December), movement between tagging and recapture loca-

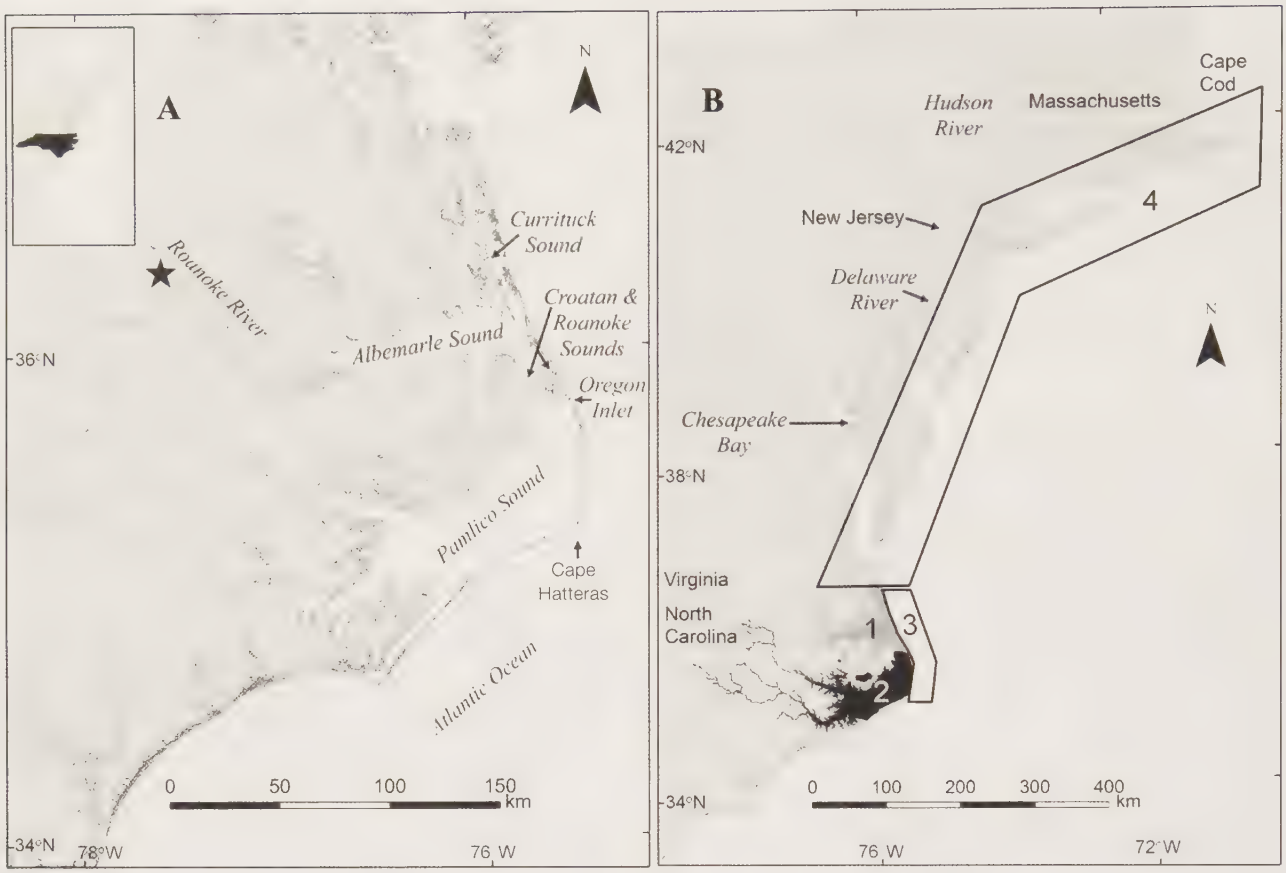

Figure 2

(A) Capture and release location (represented by the star in the upper Roanoke River) of tagged Striped Bass (*Morone saxatilis*) during the period of 1991–2008 and reference map for waterbodies in coastal North Carolina. **(B)** Geographic areas of recapture used in data analyses: 1) Albemarle Sound estuary (area shaded in gray), 2) Pamlico Sound estuary (area shaded in black), 3) North Carolina ocean waters (box 3), and 4) northern coastal waters (box 4).

tions could be known to occur during a given year. This restriction allowed movements (recapture area) to be directly related to stock abundance, which was estimated on an annual basis (i.e., each calendar year) from 1991 to 2008, the terminal year in the assessment. In addition, restriction of returns to a relatively short time period at liberty (<9 months) minimized the opportunity for growth between tagging and recapture, thereby ensuring that fish lengths at tagging (the size variable used in our analyses) were representative of the size of fish when movement occurred.

To reach another recapture area (outside the Albemarle Sound estuary), tagged fish would have had to travel a considerable distance (>300 km) from their release site in the upper Roanoke River. Therefore, to reduce the likelihood of underestimation of fish movement, we excluded tag returns from the first 14 days at liberty, affording tagged fish a more realistic period of time to complete movement or migration to another system. Indeed, the earliest tag return from outside the Albemarle Sound estuary (in North Carolina ocean waters) occurred at 16 days after tagging, providing justification for our 14-day exclusion window. Finally, data from 1994 were excluded from analyses because of reduced tagging efforts in that year (only 9 fish were tagged and 1 returned).

To determine which explanatory variables affected movements of Striped Bass and to assess their relative importance, we used an information-theoretic approach. A multinomial logistic regression model was run for each of the 5 possible combinations of explanatory variables: 1) length, abundance, length×abundance (interaction model), 2) length and abundance, 3) length only, 4) abundance only, and 5) intercept only (no effects model). Akaike's information criterion (AIC) values were obtained for each candidate model. We considered the model with the lowest AIC value as the most parsimonious or "best," but we also computed additional diagnostics, Akaike differences (Δ_i) and Akaike weights (w_i), to assess how other models performed in comparison to this single best model (Burnham and Anderson, 2002). The first of these other diagnostics was calculated as

$$\Delta_i = AIC_i - AIC_{\min},$$

where AIC_i = the AIC value of a given model (i); and
AIC_{min} = the AIC value of the best model (minimum AIC).

As a general guideline, models with Δ_i close to zero have considerable empirical support, models with Δ_i of 4–7 have much less support, and models with Δ_i of 9–14 have little support (Anderson, 2008). The following equation was used to calculate w_i values:

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{r=1}^{R}\exp\left(-\frac{1}{2}\Delta_r\right)}.$$

Note that R refers to the set of models being evaluated. Values of w_i can be interpreted as the probability that a particular model (i) is the best model for the data set given that one of the models must be selected as the best (Anderson, 2008).

We based our inferences on parameter estimates from the model (i.e., on the combination of explanatory variables) deemed most parsimonious from AIC diagnostics. For example, if the third model (length effect only) was determined to be the best model, values of the parameters (i.e., regression coefficients) that represented the effect of fish length were used to calculate the predicted relative probability of Striped Bass being recovered in each recapture area as a function of their size at tagging. We assessed the fit of the best model through the use of both Pearson and deviance goodness-of-fit tests. Because explanatory variables were continuous, it was necessary to group data for these tests (Agresti, 1996). For this purpose, we used 100-mm bins and abundance bins of 0.1 million fish. All statistical analyses were performed in SAS, vers. 9.1.3 (SAS Institute, Inc., Cary, NC) with α =0.05.

Results

Tag return summary

From 1991 to 2008, 1197 tagged Striped Bass were reported as having been recaptured within their first 9 months at liberty (late April–December); analyses conducted for this study were based on data from these individuals. Hook-and-line (recreational) anglers accounted for a majority (84%) of tag returns. Although most returns (80%) were from fish 400–600 mm TL (at tagging), fish lengths ranged from 287 to 1105 mm TL. Moreover, nearly all tag returns (154 of 156) of larger Striped Bass (>600 mm TL) were from years in which stock abundance exceeded 1.5 million fish (Table 1).

Temporal recapture trends

The AR stock of Striped Bass increased their movement outside of the Albemarle Sound estuary as the

Table 1

Number of tag returns of Striped Bass (*Morone saxatilis*) per combination of total annual stock abundance (millions of fish) and interval of total length (TL) at tagging. Annual abundance estimates (1991–2008) of Albemarle Sound–Roanoke River Striped Bass were obtained from a statistical catch-at-age model (NCDMF and NCWRC[2]). Only those tag returns occurring after the first 2 weeks but within the first calendar year at liberty were included in data analyses and are enumerated here. "–"=no tag returns for that year.

Abundance (millions)	Year	Number of returns per size (mm TL) interval							
		<400	400–499	500–599	600–699	700–799	800–899	900–999	>1000
1.035	1993	–	37	15	–	–	–	–	–
1.101	1991	10	17	5	–	–	–	–	–
1.104	1992	2	48	7	1	1	–	–	–
1.388	1995	–	4	17	–	–	–	–	–
1.518	2005	1	68	36	7	2	–	6	–
1.569	1996	4	7	13	1	–	–	–	–
1.673	2004	–	17	8	–	1	3	1	–
1.752	1997	6	38	28	4	1	–	–	–
1.803	2006	–	54	80	6	5	3	9	3
1.828	2003	7	20	36	7	2	1	3	–
1.829	2001	1	35	38	12	2	2	–	–
1.836	2000	1	29	16	4	2	–	–	–
1.860	2002	2	27	39	4	7	1	–	1
1.877	1998	4	41	23	7	3	–	–	–
1.895	2008	38	42	13	3	–	3	5	6
1.907	1999	1	29	17	5	1	–	–	–
2.051	2007	–	19	40	11	3	1	5	2

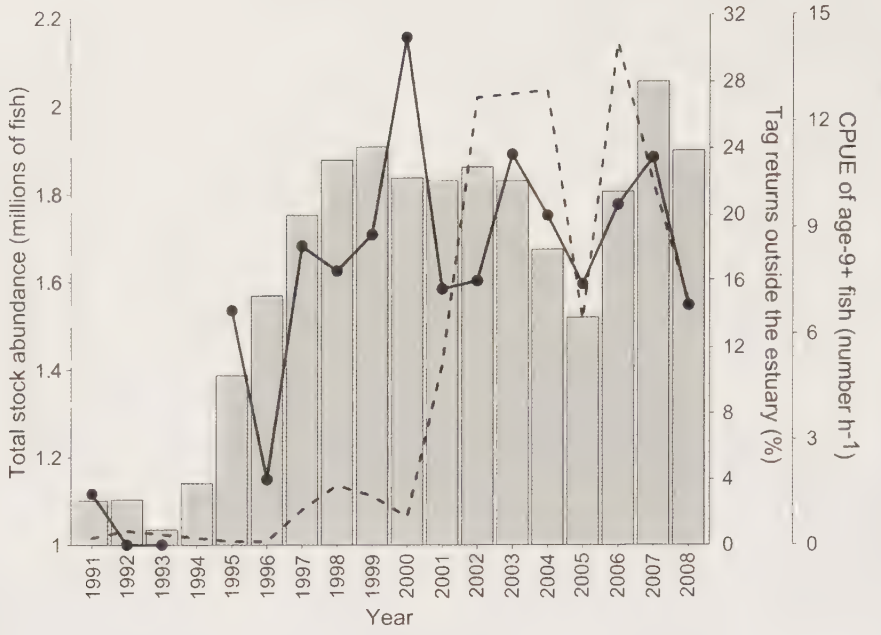

Figure 3

Time series for the period of 1991–2008 of the following trends of the Albemarle Sound–Roanoke River stock of Striped Bass (*Morone saxatilis*): 1) total annual abundance (millions of fish; gray bars) of the stock (age 1+ fish) estimated from a statistical catch-at-age model (NCDMF and NCWRC[2]), 2) annual percentage of tag returns (solid line) that occurred outside the Albemarle Sound estuary from Striped Bass tagged and released on the spawning grounds in the upper Roanoke River, and 3) catch per unit of effort for fish (number h^{-1}) age 9+ (>700 mm in total length) (dashed line) in annual spring electrofishing surveys on the Roanoke River spawning grounds.

population rebuilt over the past 2 decades (1991–2008). In the early 1990s, few tag returns occurred outside the Albemarle Sound estuary: <4% annually across the years of 1991–96, with the exception of 1995 (Fig. 3). However, as the stock increased in abundance and its age structure expanded, returns from regions outside the Albemarle Sound estuary increased considerably and ranged from 15% to 31% annually during the years of 1997–2008 (Fig. 3).

Effects of fish size and stock abundance on recapture area

Fish size and stock abundance affected recapture area. The best multinomial logistic regression model included the main effects of both fish length and stock abundance but not their interaction (Table 2). Goodness-of-fit tests indicated this model fitted the sample data well (Pearson goodness of fit, χ^2=117, degrees of freedom=126, P=0.70; deviance goodness of fit, χ^2=104, degrees of freedom=126, P=0.93). Although the best model showed that recapture area depended on both fish size and stock abundance, AIC diagnostics across the suite of models indicated that fish length exerted a much stronger effect than abundance. Specifically, the model that included only fish length had moderate empirical support (Δ_i=3.8, w_i=0.12), but the model that included stock abundance alone had very little support (Δ_i=462.2, w_i=0) (Table 2).

Striped Bass of the AR stock exhibit a strong size-dependent migration pattern, whereby both the incidence of emigration and the distance emigrants move increase with fish size. The best model predicted that the probability of emigration from (i.e., recapture outside) the Albemarle Sound estuary increased dramatically with fish size. Specifically, the probability of recapture within Albemarle Sound declined sharply (from values >90%) beyond 600 mm TL, the size at which recapture probabilities began to increase in other areas, such as Pamlico Sound and ocean waters (Fig. 4). The model predicted that Striped Bass 700–800 mm TL in length were most likely to be recaptured in ocean waters of North Carolina (Fig. 4C) and that the largest fish (>850 mm TL) were most likely to be recaptured in the northern coastal region (Fig. 4D).

Empirical tag return data supported the movement pattern indicated by the best model. Nearly all (92%) of the tag returns of smaller fish (<600 mm TL;

Table 2

Diagnostics with Akaike's information criterion (AIC) for candidate multinomial logistic regression models that relate the recapture area (Albemarle Sound estuary, Pamlico Sound estuary, North Carolina ocean waters, or northern coastal waters from Virginia to Massachusetts) of tagged Striped Bass (*Morone saxatilis*) to fish length and total annual stock abundance for the years 1991–2008. Each model represents a different combination of these explanatory variables. Note that Δ_i=Akaike's differences and w_i=Akaike's weights, where lower values of Δ_i and higher values of w_i indicate greater relative empirical support for a model.

Model	AIC	Δ_i	w_i
Length + abundance	1003.2	0.0	0.80
Length only	1007.0	3.8	0.12
Length + abundance + length *x* abundance	1007.8	4.6	0.08
Abundance only	1465.4	462.2	0.0
Intercept only	1496.1	492.9	0.0

n=1040) occurred within the Albemarle Sound estuary (Fig. 5A). Yet, only 47% of returns of fish 600–799 mm TL (n=102) and 2% of returns of fish >800 mm TL (n=55) occurred in Albemarle Sound; most tag returns of these larger fish occurred in ocean waters (Fig. 5, B and C). Interestingly, the majority (78%) of tag returns of the largest fish in this study (800–1105 mm TL) occurred in distant coastal waters from New Jersey to Cape Cod, 780 to 1250 km from the release site (Fig. 5C).

Stock abundance also affected the areas in which Striped Bass were recaptured. The best model predicted a slight increase (~5%) in recapture of small Striped Bass (<600 mm TL) in the Pamlico Sound region as stock abundance increased from 1 to 2 million fish (Fig. 4B). This trend also was evident in empirical tag return data. Returns from the Pamlico Sound estuary, ~6% of all returns, occurred only during years in which stock abundance exceeded 1.4 million fish. There were no returns from the Pamlico Sound estuary during years of lower abundance (1.0–1.1 million fish) (Fig. 6).

Discussion

Continuous tagging over a 20-year period, a length of effort that is rare in most fisheries, allowed us to determine the strong effect of fish size and relatively smaller effect of stock abundance on a fish stock's spatial distribution. Multiple stocks of Striped Bass co-occur along the East Coast of the United States during nonspawning periods. Therefore, by tagging fish on their natal spawning grounds (when stocks are separated), we were able to investigate stock-specific movements and spatial distribution—information that could otherwise not have been resolved with approaches such as fisheries-independent surveys (e.g., trawl surveys). In this section, we provide further details on the effects of fish size and stock abundance on the spatial distribution of the AR stock of Striped Bass and on the implications for management of Striped Bass.

Effects of fish size on recapture area

The increase in tag returns of the AR stock from regions outside its natal estuary over the past 2 decades was largely due to expansion of the age and size structure of the stock as it recovered. The majority of returns (67%) that occurred outside the Albemarle Sound estuary during the stock recovery period were from ocean waters. Model results and empirical data both showed the probability of Striped Bass being recaptured in ocean waters increased dramatically with fish size beyond 600 mm TL, to the point where the largest individuals (>800 mm TL) were almost exclusively captured in ocean waters. Therefore, it is not surprising that returns from ocean waters increased over the past 2 decades as more fish from this largest size class (which was the class most likely to emigrate to ocean habitats) became available for tagging and recapture as the age and size structure of the AR stock expanded.

The strong size-dependent emigration pattern of Striped Bass revealed by this study helps explain the lack of recaptures in ocean waters by Hassler et al.[1], who also focused on the AR stock. To collect fish for tagging, Hassler et al.[1] primarily used small-mesh (<150 mm stretched) gill nets that likely selected for smaller fish. Indeed, of the 2428 returns in their study, most (86%) were from fish 400–550 mm TL at tagging, and only 2 returns (<0.1%) were from fish >800 mm TL at tagging. Moreover, the vast majority (88%) of tag returns in their study occurred within the first year at liberty. Therefore, given the small sizes of tagged fish and short-term nature of returns (i.e., small tagged fish did not have time to grow into larger size categories because of high har-

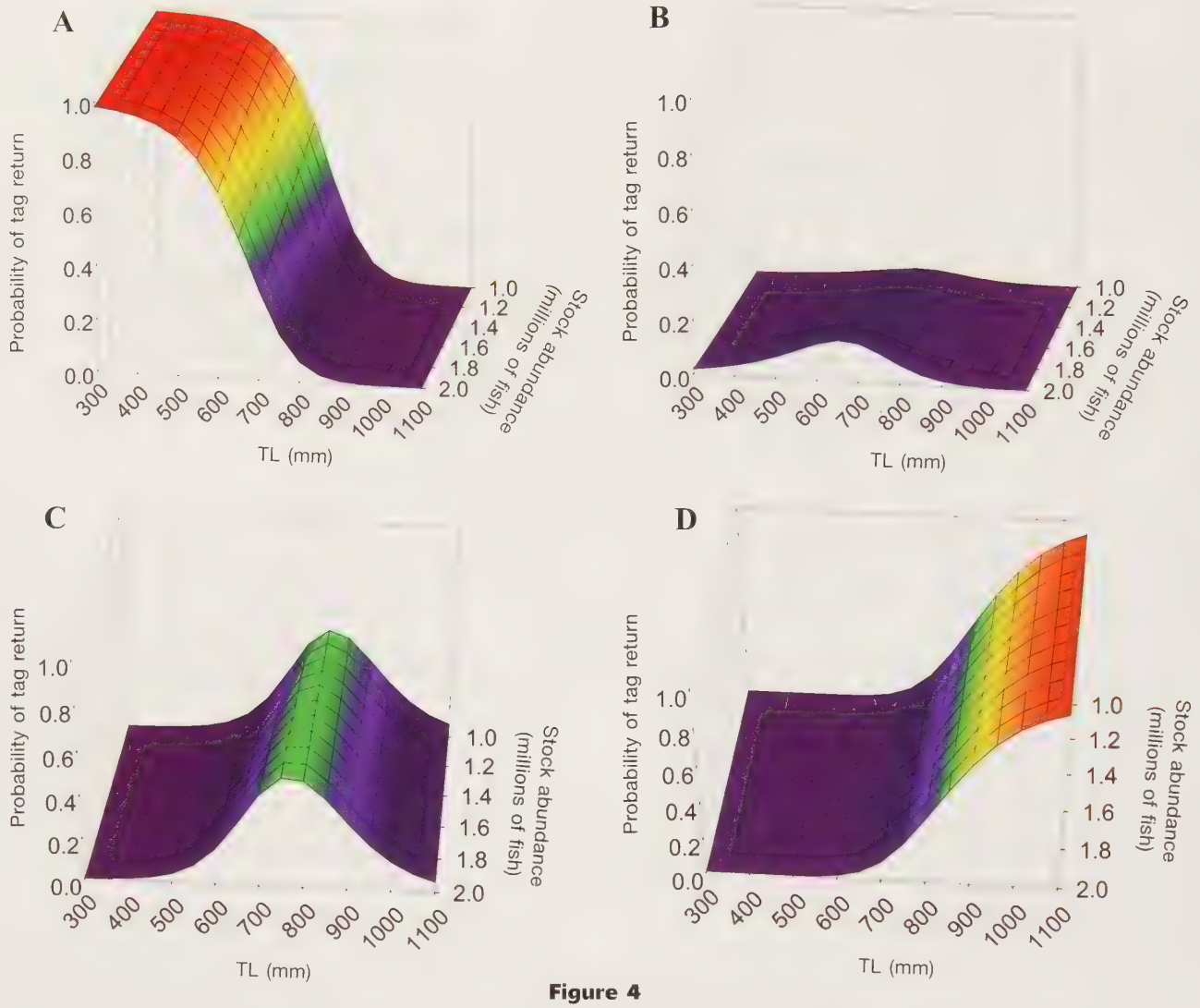

Figure 4

Predicted probabilities of tag returns in each recapture area as a function of total length (TL) and annual total stock abundance (millions of fish) of Striped Bass (*Morone saxatilis*) during the period of 1991–2008. We used the following 4 recapture areas **(A)** Albemarle Sound estuary, **(B)** Pamlico Sound estuary, **(C)** North Carolina ocean waters, and **(D)** northern coastal waters (for locations, see the map in Fig. 2B). Probabilities are based on parameter estimates from the most parsimonious multinomial logistic regression model that related the recapture area of Striped Bass to TL and stock abundance. Cooler and warmer colors represent low and high tag return probabilities, respectively, as follows: (0.0, ■; 0.2, ■; 0.4, ■; 0.6, ■; 0.8, ■; 1.0, ■). Note that tag return probabilities sum to 1.0 (across recapture areas) for a given combination of TL and stock abundance.

vest), the lack of ocean recaptures by Hassler et al.[1] is not surprising. Nearly all fish recaptured in their study (>99%) were smaller than the size at which appreciable ocean emigration occurs (>800 mm TL), as indicated in our study.

Although other factors, such as prey availability and susceptibility to predation, may be involved, water temperature appears to be a salient factor in explanation of the size-dependent migration and distribution patterns of the AR stock. A change in temperature preferences with fish size has been hypothesized to be the main driver of the size-dependent emigration pattern observed previously for other stocks of Striped Bass (Coutant, 1985), especially the Chesapeake stock (Dorazio et al., 1994; Secor and Piccoli, 2007).

Decreases in temperature optima with fish size can be explained by bioenergetic principles. Specifically, the temperature threshold beyond which the increase in total metabolic load starts to become stressful (i.e., the point at which the scope for activity and growth begins

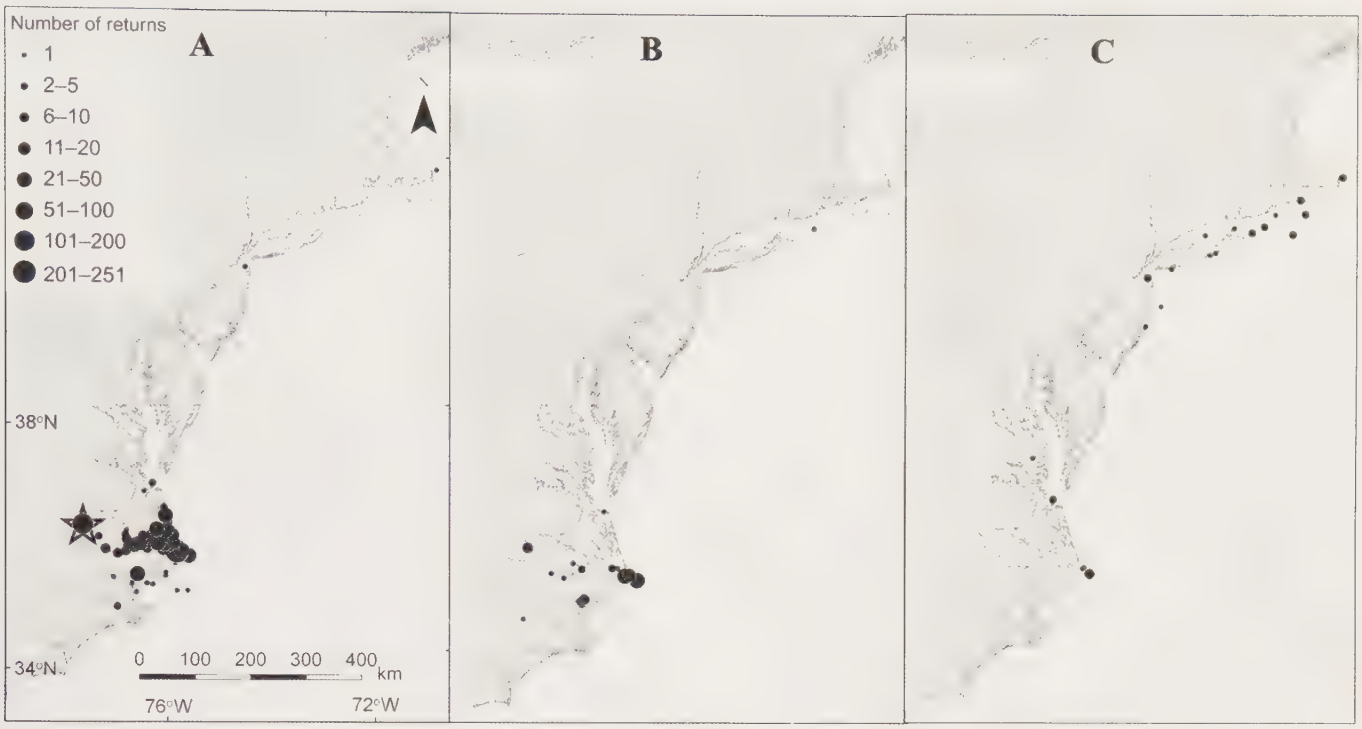

Figure 5

Tag return locations of Striped Bass (*Morone saxatilis*) along the eastern seaboard of the United States by length group (data pooled across years): **(A)** fish 287–599 mm in total length (TL) (n=1020 returns), **(B)** fish 600–799 mm TL (n=101 returns), and **(C)** fish 800–1105 mm TL (n=55 returns). Bubble sizes represent the number of tag returns from each location (within each length group). The star in panel A denotes the location where Striped Bass were tagged and released during annual spring electrofishing surveys conducted in the Roanoke River in 1991–2008. Only those tag returns that occurred after the first 2 weeks but within the first calendar year at liberty were included in analyses and are shown. The location of 21 tag returns (of the 1197 total) could be assigned only to 1 of the 4 broad geographic recapture areas (shown in Fig. 2B) and are, therefore, not shown.

to decline) occurs at progressively lower temperatures as fish size increases because larger individuals have a greater total metabolic demand than smaller individuals on the basis of body size alone (Hartman and Brandt, 1995). Therefore, after spawning, most large Striped Bass may emigrate, as we found, to cooler northern ocean habitats, which would provide a metabolic reprieve, rather than spend their summers in warm estuarine waters.

Interestingly, Striped Bass of the AR stock in the intermediate size range of 700–850 mm TL, were mainly recaptured in ocean waters off North Carolina, from the Oregon Inlet north to the border of North Carolina and Virginia. No Striped Bass were recaptured in ocean waters south of Cape Hatteras, where summer temperatures (>26°C; http://www.ndbc.noaa.gov, Station#41036) are similar to summer temperatures in Albemarle Sound. Therefore, nearby ocean waters may provide an adequate thermal refuge (23–26°C; http://www.ndbc.noaa.gov, Station#44100) during summer for Striped Bass in the size range of 700–850 mm TL. One intriguing question is whether the size at which the onset of ocean emigration occurs will shift to a smaller size as inshore estuarine waters, which already approach 30°C in summer (http://waterdata.usgs.gov, Gage#0208114150), are expected to continue warming under current projections for climate change (IPCC, 2007). Continuation of the long-term tagging program on the AR stock of Striped Bass could help address this question.

Previous research on northern stocks of Striped Bass has provided evidence for diverse lifetime migration patterns: some members of a given population reside in freshwater or estuarine environments throughout their life (resident contingent) and others are more exploratory and engage in large-scale coastal migrations (migratory contingent) (Clark, 1968; Secor, 1999). There is particularly strong evidence for this "contingent" behavior in Striped Bass in the Hudson River (Secor and Piccoli, 1996; Secor et al., 2001; Zlokovitz et al., 2003). Our study, however, provides little indication of this phenomenon in the AR stock of Striped Bass. If contingent behavior had been prevalent, one would have expected that some large fish would have remained and been recaptured in the Albemarle Sound after spawning. Yet, of the 50 fish exceeding 855 mm TL that were recovered in our study, none were recaptured within Albemarle Sound and, instead, all were taken in the ocean. It is possible that contingent behavior is not

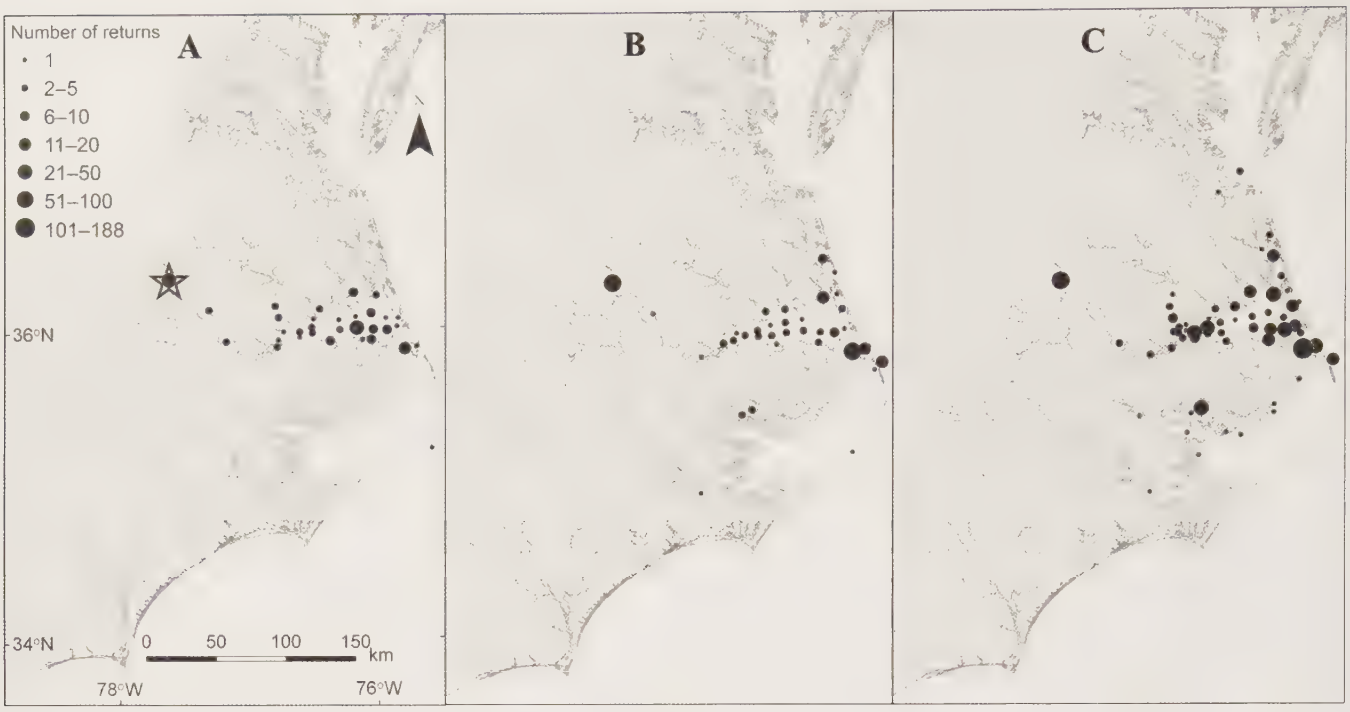

Figure 6

Tag return locations of Striped Bass (*Morone saxatilis*) <600 mm in total length in North Carolina and Virginia coastal waters by stock abundance in the year of release: **(A)** annual abundance values of 1.0–1.1 million fish (n=138 returns), **(B)** annual abundance values of 1.4–1.7 million fish (n=169 returns), and **(C)** annual abundance values of 1.8–2.0 million fish (n=713 returns). Bubble sizes represent the number of tag returns from each location (within each abundance group) as indicated in the legend. The star in panel A denotes the location where Striped Bass were tagged and released during annual spring electrofishing surveys in the Roanoke River in 1991–2008. Only those tag returns that occurred after the first 2 weeks but within the end of the first calendar year at liberty were included in analyses and are shown. The location of 20 tag returns (of the 1040 total) could be assigned to only 1 of the 4 broad geographic recapture areas (shown in Fig. 2B) and are, therefore, not shown.

beneficial, and, therefore, it does not manifest in the AR stock because of high inshore water temperatures during summer that would be unsuitable for "resident" fish once they attain a large size. The possibility for latitudinal differences in the frequency of contingent behavior in Striped Bass and other fishes warrants future investigation.

Effects of stock abundance on recapture area

Stock abundance in the year of release was included in the best model explaining where Striped Bass were recaptured. This effect was primarily a result of smaller Striped Bass being recaptured in the adjacent estuarine systems of Pamlico Sound and lower Chesapeake Bay only in the years of highest abundance (Fig. 6C). Also, evidence of recapture patterns within the Albemarle Sound estuary were indicative of a density effect. Namely, tag returns were much more common in the eastern portions of Albemarle Sound, particularly in Currituck Sound (6% vs. 1% of returns) and Croatan and Roanoke sounds (32% vs. 6%), during years in which stock abundance exceeded 1.4 million fish in contrast to years when it was below this level (Fig. 6). Therefore, although adults generally may remain inshore until they reach larger sizes (>600 mm TL), the distances they disperse *within* estuarine habitats, after spawning, tend to increase with the abundance of conspecifics, presumably because of density-dependent mechanisms. These movements likely are important ecologically to prey of Striped Bass because the smallest size groups (<600 mm TL) are the most numerous in this population (i.e., predation effects may change with stock abundance). Future research should investigate these possibilities and better isolate the effects of density by controlling for environmental covariates, such as the abundance of competitor species and changing habitat suitability, as suggested by Shepherd and Litvak (2004).

Management implications

Results from this study have important implications for the management of Striped Bass along the East Coast of the United States. With current assessment strategies, Striped Bass from the AR stock are assumed not to contribute to the Atlantic Ocean mixed stock

fishery (ASMFC[4]). However, this study revealed that some members of the AR stock, those fish surviving to sizes >800 mm TL, are indeed migratory and, therefore, unequivocally contribute to (i.e., are harvested by) the mixed stock fishery of the Atlantic coast. Because management benchmarks for the mixed stock fishery, such as the threshold fishing mortality (F_{MSY}=0.41; ASMFC[4]), currently are based on data from Chesapeake, Hudson, and Delaware stocks that are potentially more productive than the AR stock, it is possible that the mixed stock fishery could affect the AR stock disproportionately. Accordingly, future research should establish the productivity of the AR stock of Striped Bass in relation to other stocks. If the AR stock is found to be less productive, then future work also should determine the implementation costs of more stringent fishing regulations in the mixed stock fishery, namely the amount and value of harvest that would be lost from more productive stocks (Chaput, 2004; Crozier et al., 2004; Hilborn et al., 2004).

Results from this study also have implications for the assessment and management of Striped Bass within North Carolina. Currently, landings of Striped Bass outside the Albemarle Sound estuary (region 1; Fig. 2B) are not included in the AR stock assessment (NCDMF and NCWRC[2]). Stock status is based on the estimate of fishing mortality ($F_{threshold}$=0.27) for fully recruited Striped Bass of age 4–6 and 400–600 mm TL, a size group for which fish were found in this study to increase their movement to adjacent estuarine systems outside the stock boundary as they increased in abundance. Therefore, by not including fish that move to and are harvested in adjacent systems, the AR stock assessment underestimates fishing mortality. Accordingly, future research should examine the sensitivity of fishing mortality estimates from the AR stock assessment to additional landings of age-4–6 Striped Bass of AR origin outside the Albemarle Sound estuary.

Caveats

It is important to note that the analyses in this study indicate the probability of recapture location; movements are inferred from these data. Fishermen behavior (e.g., spatiotemporal differences in fishing effort or size targeting because of regulations and economic value) can affect and potentially bias tag returns and inferences about movement patterns (Hilborn, 1990; Gillanders et al., 2001). The size-dependent migration pattern that we observed could be due to differences in selectivity between ocean and estuarine fisheries; that is, small tagged fish could have migrated to the ocean but not been caught in the fishery. However, fisheries-independent data indicate that it is predominantly the large Striped Bass of the AR stock that migrate to ocean waters. In a mobile telemetry study, Haeseker et al. (1996) searched the Albemarle Sound during summer (May–August) for the presence of 26 telemetered Striped Bass (all but 1 fish <600 mm TL) that participated in the April Roanoke River spawning run. They relocated 25 (96%) of these fish in the Albemarle Sound at least 1 month after spawning, providing evidence that smaller Striped Bass mostly remain in the estuary after spawning. Furthermore, in an ongoing telemetry study, 163 Striped Bass ranging in length from 445 to 1146 mm TL (mean=580 mm TL) were telemetered in the Roanoke River during spring, beginning in 2011, by Harris and Hightower.[5] Most large fish in their study (15 of the18 individuals >900 mm TL at tagging) have been detected by coastal receiver arrays in Massachusetts, New York, New Jersey, Delaware, and Virginia, but no smaller individuals have been detected in these northern ocean waters (Harris and Hightower[5]). Hence, results from these fisheries-independent telemetry studies corroborate the strong size-dependent emigration pattern of the AR stock of Striped Bass that we inferred from tag recaptures in our study.

A limitation of our study was that nearly all tag returns (99%) from larger fish (>600 mm TL) occurred during years of higher stock abundance (>1.5 million fish). Therefore, it is possible that the observed ocean emigration of larger fish was due in part to the higher abundance of similar size conspecifics (i.e., density-dependent mechanisms). However, ocean emigration of the AR stock of Striped Bass appears to be a size-dependent phenomenon related to bioenergetics as described and is probably largely independent of ambient population density or abundance. Two lines of evidence support this notion. First, data on large Striped Bass (>600 mm TL) across the more restricted range of annual values of stock abundance (1.5–2.0 million fish) indicate that density had little effect (an increase <3%) on the probability of large fish being recaptured in ocean waters. Second, just as we found in our study, Dorazio et al. (1994) found a strong size-dependent emigration pattern for the Chesapeake Bay stock: most fish >800 mm TL were recovered in northern ocean waters from New Jersey to Maine. Their study occurred in 1988–91, years when the Chesapeake Bay stock was at relatively low abundance levels and still rebuilding, demonstrating that substantial ocean emigration of large fish, albeit from a different stock, still occurs at low densities.

[4] ASMFC (Atlantic States Marine Fisheries Commission). 2003. Amendment 6 to the Interstate Fishery Management Plan for Atlantic Striped Bass. Fishery Management Report No. 41 of the Atlantic States Marine Fisheries Commission, 63 p. [Available from http://www.asmfc.org/uploads/file/sbAmendment6.pdf.]

[5] Harris, J. E., and J. E. Hightower. 2013. Unpubl. data. North Carolina Cooperative Fish and Wildlife Research Unit, U. S. Geological Survey, and Department of Applied Ecology, North Carolina State Univ., Raleigh, NC 27695.

Conclusions

Our study revealed major changes in the movements and associated distribution of a fish stock as it recovered from a depleted state. During the early phases of rebuilding, the stock was largely confined to its natal estuary but dramatically expanded its distribution, and degree of anadromy, as recovery continued. This major shift in distribution was due to changes in the demographics—namely size structure and total abundance—of the stock as it recovered. Size structure has received little attention in the fisheries literature in regard to its effects on stock distribution but appears to be important.

Although the recovery of Striped Bass often is regarded as one of the few success stories in fisheries management (Richards and Rago, 1999), many global fish stocks are either currently experiencing rebuilding or have recently recovered, for example, nearly one-third of the 166 stocks examined worldwide by Worm et al. (2009). It is possible that the spatial dynamics of these and other rebuilding stocks will differ from their depleted state. For instance, as stocks recover and more individuals are allowed to reach larger sizes (e.g., through a reduction in fishing mortality; Berkeley et al., 2004), the spatial distribution of stocks may shift or expand because larger, older fish often have different migratory behaviors and habitat preferences than smaller, younger individuals (Heifetz and Fujioka, 1991; Macpherson and Duarte, 1991; Shepherd et al., 2006; Grüss et al., 2011). Such changes in the movement and distribution of fish populations can have important consequences for stock assessments, as argued previously, and also affect ecosystem dynamics (e.g., as predators move into new areas, they can exert top-down changes in community structure; Casini et al., 2012). Therefore, resource managers should be aware of potential changes in the movement and distribution of recovering fish stocks and account for them accordingly if they manifest. As indicated in our study, long-term tagging and monitoring data are useful for detection of population-level changes in the movement and distribution of fishes.

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Residence time and habitat duration for predators in a small mid-Atlantic estuary

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Abstract—Residence times of individual fishes should reflect the durations over which habitat resources support survival, metabolic maintenance, and adequate growth. From May to October in 2006 and 2007, we measured residencies of ultrasonically tagged age-1+ Striped Bass (*Morone saxatilis*; n=46), age-0 and age-1+ Bluefish (*Pomatomus saltatrix*; n=45 and 35) and age-1+ Weakfish (*Cynoscion regalis*; n=41) in a small estuarine tributary in New Jersey with 32 ultrasonic receivers to monitor movements and sensors to measure habitat resources. Striped Bass and age-1+ Bluefish used the estuary for medians of 9.5 days (d) (max=58 d) and 22 d (max=88 d), and age-0 Bluefish and Weakfish were resident for medians of 30 d (max=52 d) and 41 d (max=88 d), respectively. Small individuals <500 mm TL were likely to remain in the estuary longer at warmer temperatures than were large individuals. Size-dependent temperature responses were similar to optimal temperatures for growth reported in previous studies. Freshwater discharge also influenced residence time. All species were likely to remain in the estuary until freshwater discharge rates fell to a value associated with the transition of the estuarine state from a partially to fully mixed state. This transition weakens flows into the upstream salt front where prey concentrations usually are high. Time of estuarine residence appeared to be regulated by temperatures that controlled scopes for growth and the indirect effects of freshwater discharge on prey productivity and concentration. Changes in the seasonal phenology of temperature, precipitation, and human water use could alter the durations over which small estuarine tributaries serve as suitable habitats.

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Temperate estuaries serve as spawning, nursery, and feeding habitats for many fishes and invertebrates during warmer months (Mann, 2000; Able, 2005; Able and Fahay, 2010). Warm temperatures, high nutrient-stimulated primary and secondary productivity, and abundant spatial or structural refuges from predation enhance growth and survival. However, because estuaries are shallow, semi-enclosed bodies of water along the land–sea boundary, high-frequency atmospheric variability is rapidly translated into variability in biophysical processes that regulate the vital rates of species (e.g., water temperature, freshwater discharge, nutrient inputs, circulation and retention, and dissolved oxygen). Estuarine habitat suitability is, therefore, largely controlled by atmospheric and tidal forcing. As a result, estuarine habitat suitability is dynamic, and suitable habitats have temporal dimensions of timing and duration that are as important as the spatial dimensions of location and volume (Livingston, 1987; Manderson et al., 2002; Manderson et al., 2003; Manderson et al., 2006; Peterson et al., 2007).

Animals move in variable environments to fulfill requirements for survival, metabolic maintenance, growth, and reproduction and are believed to "climb" local fitness gradients that fall within their perceptual ranges (Armsworth and Roughgarden, 2005). Individual animals should minimize movement costs by becoming resident in suitable habitats until more costly long-distance movements are required by changes in habitat resources, such as temperature, oxygen concentrations, and concentrations of predators or prey or by life history event schedules. Changes in atmospheric forcing (e.g., air temperature and precipitation) that change both the timing and persistence of suitable shallow coastal habitats should affect the movement costs and energy budgets of the individual animals that use them. Because changes in atmospheric forcing and hydrography are coherent over spatial scales of 100s to 1000s of kilometers (Hare and Able, 2007; Manderson, 2008; Shearman and Lentz, 2010), effects on energy budgets of individual animals are likely to affect demographic rates at the population level.

In this study, we used passive ultrasonic biotelemetry and environmental monitoring to measure relationships of residence and egress of 3 predators—Striped Bass (age-1+ *Morone saxatilis*), Bluefish (age-0

and age-1+ *Pomatomus saltatrix*) and Weakfish (age-1+ *Cynoscion regalis*)—to habitat conditions in a small mid-Atlantic estuarine tributary that serves as a summer feeding and nursery ground. Individuals of these 3 species undertake broad-scale seasonal migrations of 100s to 1000s of kilometers along the Atlantic coast of the United States but can exhibit site fidelity in summer feeding and nursery habitats (Ng et al., 2007; Taylor et al., 2007; Pautzke et al., 2010; Turnure, 2010). They occupy upper trophic levels in mid-Atlantic estuarine food webs and are responsible for the transfer of nutrients and energy between benthic and pelagic compartments within estuaries and between estuaries and the coastal ocean (Hagy, 2002; Krause et al., 2003; Johnson et al., 2009).

We report on the seasonal and size-dependent patterns of residency of these predators in a small tributary (surface area of ~1000 ha) in New Jersey over 2 years. We use generalized additive mixed models to quantify size-dependent relationships of time of estuarine residence to water temperature and freshwater discharge. We assume that residency and flux rates of individuals through the estuary reflect the timings and durations when habitat resources support survival, metabolic maintenance, and at least adequate growth, except when emigration is triggered by changes in requirements associated with life-history-event schedules (e.g., timing of spawning) (Charnov, 1976; Winkler et al., 1995; Belisle, 2005).

Materials and methods

Study area

We performed acoustic biotelemetry in the Navesink River, New Jersey, a tributary of the Hudson-Raritan Estuary (Fig. 1), described in detail in other studies (Shaheen et al., 2001; Stoner et al., 2001; Scharf et al., 2004; Manderson et al., 2006). The Navesink River is nearly 1.5 km wide and extends ~12 km east from its primary freshwater source, the Swimming River, to the Shrewsbury River and then to the Hudson-Raritan Estuary where it connects to the Atlantic Ocean. Salinities range from as low as 0.08‰ at the head of the Swimming River to ~27‰ at the confluence of the Navesink and Shrewsbury rivers. The tidal range averages 1.4 m. Tidal currents are flood dominated and attenuate in the middle and upper river, an area that is both deeper (mean depth [μ D]=1.5 m mean low water [MLW]; maximum of ~9 m) and has sediments of finer grains than the lower river (μ D=1.0 m MLW; maximum of ~6 m) (Chant and Stoner, 2001; Fugate and Chant, 2005). The lower river has a complex network of channels flanked by sandbars and vegetated coves.

Infrastructure of the estuarine observatory

Fishes tagged with ultrasonic transmitters were detected with an array of omnidirectional receivers (model VR2, VEMCO[1], Bedford, Canada) moored throughout the Navesink River from May 15 to October 3, 2006, and from April 18 to October 31, 2007 (Fig. 1). We attached receivers to anchored lines that had surface and subsurface floats. The subsurface floats suspended the receivers ~80 cm above the bottom. In 2006, the array consisted of 27 receivers. In 2007, we moored 5 additional receivers in several marsh creeks and coves. Nearest neighbor distances between receivers in the river averaged 493 m (standard deviation 141 m, within a range of 216–788 m). On the basis of range tests, receivers moored in the middle and upper river had detection ranges of 350–600 m. Detection ranges were smaller and more variable in the lower river, which is topographically complex. The estuarine volume monitored by the array of all moored receivers was $\sim 1.397 \times 10^7$ m^3 (surface area=932 ha) at MLW. In 2006, the receivers were retrieved in September. We subsequently discovered that a few tagged fishes remained in the estuary after the receivers were retrieved. Therefore, in 2007, receivers were left in place for an additional month.

We measured environmental variation with moored instruments and supplemental mobile surveys. The moored instruments provided measurements ~12 cm above the bottom of the seafloor at 20-min intervals and included 3 Star-Oddi (Gardabaer, Iceland) temperature, salinity, and pressure sensors; 3 YSI, Inc. (Yellow Springs, Ohio) temperature, salinity, pressure, and dissolved oxygen sensors; and an Aanderaa RCM 9 (Aanderaa Data Instruments, Bergen, Norway) meter that measured current speed and direction, temperature, salinity, pressure, and optical backscatter. Star-Oddi sensors were used throughout the system (Fig. 1). YSI sensors were deployed in the upper river where episodes of low dissolved oxygen occur. We moored the RCM 9 in the channel that connects the lower and middle rivers. Weekly hydrographic surveys were performed from a 6-m vessel through the use of a Hydrolab DataSonde probe (Hach Hydromet, Loveland, CO) with temperature and salinity sensors mounted 0.5 m below the surface of the water and integrated with a GPS, and a Sea-Bird Electronics, Inc. (Bellevue, WA) SBE 25 Sealogger CTD with temperature, conductivity, pressure, dissolved oxygen, photosynthetically active radiation, turbidity, and fluorometer sensors. During each weekly survey, we performed cross-sectional transects of the river that intercepted all receiver moorings. The Hydrolab DataSonde and GPS continuously recorded temperate, salinity, and geographic position at 1-s intervals. Vertical profiles of the water column at each mooring were measured with the conductiv-

[1] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

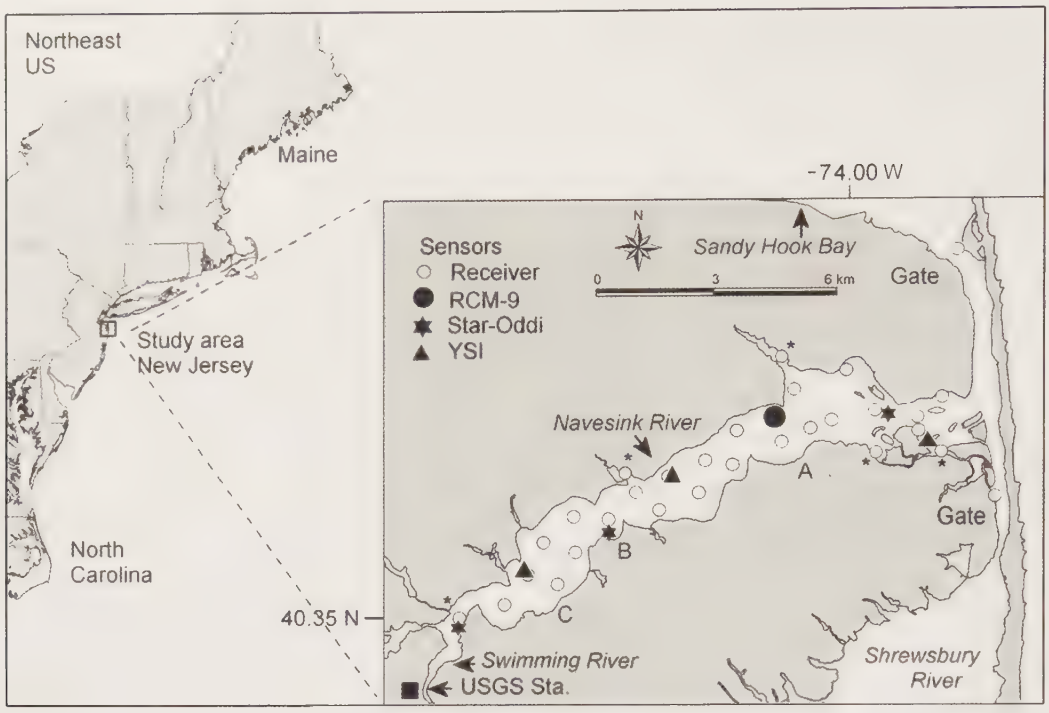

Figure 1

Map of the study area in the Navesink River, New Jersey, on the northeastern coast of the United States and the locations of the 32 moorings with ultrasonic receivers (white circles) and sensors (dark symbols) that measured the physical environment in the study area in which we captured, released, and monitored the movements of tagged Striped Bass (*Morone saxatilis*), Bluefish (*Pomatomus saltatrix*), and Weakfish (*Cynoscion regalis*) in 2006 and 2007 for a study of residence times and duration of habitat suitability for these 3 predators. The 5 moorings added in 2007 are indicated by asterisks. A, B and C labels indicate the locations referred to in the text and in the legend for Figure 2. Instruments deployed with receivers included temperature, salinity, pressure, and dissolved oxygen sensors from YSI, Inc., temperature, salinity, and pressure sensors from Star-Oddi, and an RCM-9 meter from Aanderaa Data Instruments that measured current speed and direction, temperature, salinity, pressure, and optical backscatter. Measurements of freshwater discharge were made at the U.S. Geological Survey (USGS) stream flow station in the Swimming River.

ity, temperature, and depth (CTD) sensor. In 2007, we performed additional hydrographic surveys associated with gillnet surveys of predators and prey in the upper river.

Measurements of freshwater discharge (in meters per second) from the Swimming River were made at the U.S. Geological Survey stream flow station (http://nwis.waterdata.usgs.gov/nj/nwis/uv/?site_no=01407500&PARAmeter_cd=00065,00060). Barometric pressures, wind, and air temperatures were measured 7.5 km from the study area at the NOAA weather station in Sandy Hook, New Jersey (http://www.ndbc.noaa.gov/station_page.php?station=sdhn4).

Ultrasonic tagging

From May 14 to September 8, 2006 and from May 1 to October 2, 2007, we used hook and line to capture age-1+ Striped Bass, age-0 and age-1+ Bluefish, and age-1+ Weakfish as seasonally available within the footprint of the estuarine observatory (Table 1). On the basis of published age-length relationships, we divided Bluefish into age-0 and age-1+ age classes at a total length of 290 mm (Chiarella and Conover, 1990; Munch and Conover, 2000; Scharf et al., 2004). We transported fishes to the James J. Howard Marine Sciences Laboratory in Highlands, New Jersey, for internal tagging. Fishes were held ≤8 days (d) in tanks (2.5-m diameter, 0.35-m depth) supplied continuously with ambient estuarine water. We anaesthetized fishes with AquiS (AquiS New Zealand, Ltd., Lower Hutt, New Zealand) at a concentration of 54 mg/L. Duration of anesthesia averaged ~3 min.

After a fish was anaesthetized, we made an incision 1–2 cm long on its ventral midline and inserted into the body cavity a sterilized, uniquely coded ultrasonic transmitter (V9-6L with a frequency of 69 kHz, repetition rate of 40–120 s, dimensions of 9 mm×20 mm, weight of 2 g in water, and minimum battery life of 110 d; VEMCO). We closed incisions with 2 or 3 nylon sutures (Ethilon 30 and 40 with FS1 cutting needle, Ethi-

Table 1

Median (Md) total lengths (TL) in millimeters, number of fish released, release dates, median number of detections, and median residence times (in days) of fishes released in 2006 and 2007with ultrasonic transmitters in the Navesink River, New Jersey, for a study of residence times and habitat duration of 3 predators: age-1+ Striped Bass (*Morone saxatilis*), age-0 and age-1+ Bluefish (*Pomatomus saltatrix*), and age-1+ Weakfish (*Cynoscion regalis*). Median days detected (i.e., residence time in days) and confidence limits (CL) were calculated with right-censored Kaplan-Meier survival analysis (see Fig. 3). Significant Spearman's rank correlation coefficients (ρ) between release day and body length are shown in bold type. An asterisk (*) denotes that fishes caught by anglers before egress or detected by receivers on the last fall day of the experiment were censored (Striped Bass=1, age-0 Bluefish=4, age-1+ Bluefish=1, and Weakfish=1).

Species-and-age class	Year	Md TL (Range)	Number released	Release dates	Release date vs. length Spearman's ρ, *P*-value	Md number of detections (range)	Md days (95%CL) (range)
Striped Bass	2006	465 (359–630)	34	15May–28Jun	**0.41, 0.016**	2475 (343–20331)	16(9,28) (2–58*)
	2007	442 (342–510)	12	3May–19Jun	**0.76, 0.004**	1469 (22–3440)	8(7, ∞) (2–50)
Age-1+ Bluefish	2006	335 (310–390)	14	5Jun–16Aug	0.45, 0.107	5428 (311–17586)	19(16,42) (10–48)
	2007	455 (310–610)	21	1May–19Jun	**–0.83,<0.001**	3543 (60–21174)	29(20,46) (3–88)
Age-0 Bluefish	2006	210 (175–270)	15	27Aug–9Sep	**0.68, 0.005**	2503 (291–7889)	29(21,∞) (5–37*)
	2007	246 (222–275)	30	29Aug–21Sep	0.28, 0.140	1706 (101–6777)	29(22,37) (1–52*)
Weakfish	2006	337 (224–535)	15	13Jul–16Aug	0.32, 0.244	4040 (41–16568)	33(22,∞) (4–64*)
	2007	389 (304–500)	26	29Jun–9Oct	**–0.42, 0.034**	1708 (31–11391)	47(35,70) (6–88*)

con, Somerville, NJ). We measured the total length (TL) of each fish in millimeters and inserted unique anchor tags into the dorsal muscle. Fishes recovered from anaesthesia in ≤9 min and were monitored for 2–48 hours in flow-through laboratory tanks. We released fishes in good condition at randomly selected locations in the river. This random release approach was used to monitor initial patterns of habitat selection during the first 24–48 hours. We released ≤5 individuals of each age class for each species per week to observe movements over the broadest range of environmental conditions.

Striped Bass, Weakfish, and age-1+ Bluefish (n>12 for all classes) implanted with replica transmitters survived >120 d in the laboratory (B. Phelan and J. Rosendale, unpubl. data). Several age-0 Bluefish <170 mm TL died after implantation of replica transmitters. We, therefore, released only Bluefish >175 mm TL with active transmitters in the field.

Analyses

In this investigation, we analyzed predator residence times in and egress from the estuarine tributary rather than movements within the tributary. We eliminated data from 2 tagged fishes whose movement trajectories indicated that they died shortly after release. Then, we aggregated data collected at all receivers to calculate the presence or absence of each fish in the estuary for each day of observation. Individuals detected in the lower estuary and subsequently not detected for 24 h were considered absent. Several fishes detected at the upstream receiver in the Swimming River disappeared for a short time and then were detected in the Swimming River or upper Navesink River. We assumed these fishes had spent that time upstream of the receiver array and, therefore, had remained in the estuary. We performed all analyses with R software (R Core Team, 2013).

We estimated the number of days that tagged fishes used the estuary with right-censored Kaplan-Meier survival analysis (Bennetts et al., 2001). We censored 5 age-0 Bluefish and 1 Striped Bass detected in the estuary when receivers were removed in the fall, and 1 Weakfish caught by an angler in the Navesink River. In survival analysis, observations are censored when the study ends before the event response occurs (in this case, egress) or when an individual is removed from the study (e.g., dies) before the event response occurs.

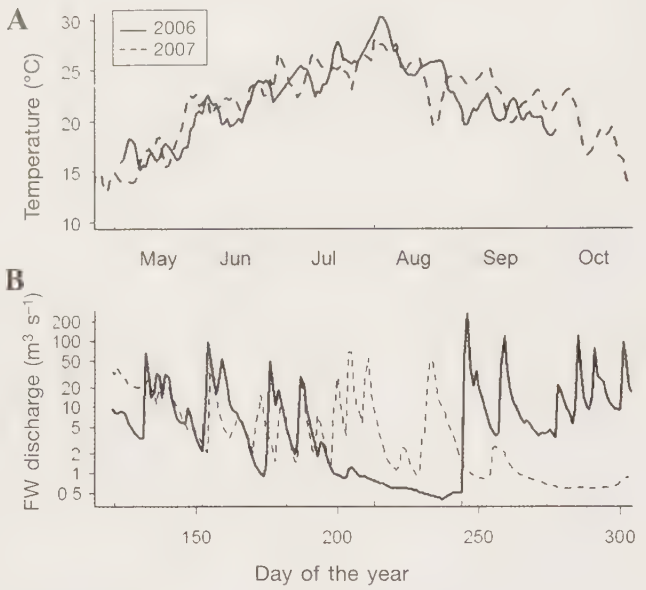

Figure 2

For a study of residence times and habitat duration of Striped Bass (*Morone saxatilis*), Bluefish (*Pomatomus saltatrix*), and Weakfish (*Cynoscion regalis*) in 2006 and 2007, mean daily (**A**) temperatures were measured at the RCM 9 sensor mooring in the Navesink River and (**B**) freshwater (FW) discharge rates (*y*-axis on log scale) were measured at a U.S. Geological Survey stream flow station in the Swimming River. For locations of the mooring and flow station, see Figure 1.

We used log-rank tests for differences in "residency" curves between the species-and-age classes and years (Harrington and Fleming, 1982).

We examined relationships between the presence of individuals in each age class of each tagged species in the estuary and environmental variation with logistic generalized additive mixed models (GAMM) in the gamm4 library in R (Aarts et al., 2008; Wood, 2012). We limited final analyses to body size and the environmental variables of water temperature and freshwater discharge, which are important drivers of the estuarine habitat suitability. Other measured environmental variables were correlated with temperature and freshwater discharge and had lower explanatory power in preliminary models. In addition, the time series for salinity and oxygen in the estuary were incomplete. Finally, complex preliminary GAMMs with more than a few variables also failed to converge.

We analyzed water temperatures measured at the RCM 9 mooring and daily freshwater discharge (cubic meters per second) measured in the Swimming River because they were the most complete and accurate time series. We log transformed freshwater discharge values, which were strongly leptokurtic. Individual fish was considered as the random effect in all models. Because the presence-absence data were serially correlated in time for each individual fish, errors were modeled as a first-order autoregressive process nested within each individual fish. Release date and year also were considered as model covariates.

Preliminary models were made with smoothing splines, and covariates were chosen through the use of manual backward selection, analysis of partial deviance, and Akaike's information criterion (AIC) (Wood, 2006). To avoid over-fitting smooths, we set gamma to 1.4 and the basis dimension (k) to 5, limiting the maximum degrees of freedom of the smooths to 4. A covariate was removed from the model if its smoother was statistically insignificant, the change in AIC was >0 when the variable was removed, or 2 standard error confidence bands in the deviance plots included zero throughout variable domain. Covariates with equivalent degrees of freedom ≈1 were tested as linear effects before they were eliminated on the basis of these criteria. We used tensor product smooths, which are appropriate when covariates are measured on different scales, to test 2-way interactions between body sizes and other significant covariates (Wood, 2006). Because the response of age-1+ Bluefish to temperature was strongly discontinuous across body sizes (i.e., lengths) at ~500 mm TL, we pooled individuals into 2 body-size classes (300–500 mm TL, >500 mm TL) and treated body size as a factor covariate.

Results

Patterns of temperature and freshwater discharge

Spring and summer of 2006 were hotter and drier than those seasons in 2007 (Fig. 2, A and B). In 2006, spring warming rates were slightly higher and, in late July–early August, temperatures exceeded 30.0°C (2006 max=30.2°C; 2007 max=28.0°C). During the autumn, however, temperatures were cooler in 2006 than in 2007. Discharge in the Swimming River was high during the spring of both years. Freshwater discharge was low (<2 m^3 s^{-1}) and discharge events were relatively rare from mid-July through August 2006. In 2007, periods of low discharge occurred briefly (2–3 d) once in July and twice in August. Discharge was low throughout much of the fall of 2007, in contrast to several episodes of high river discharge that were produced by frequent rains during the autumn of 2006.

Patterns of release

The species-and-size classes were available for collection and release during different periods of time (Table 1). Striped Bass were released in May and June. We released age-1+ Bluefish from May to July, but large

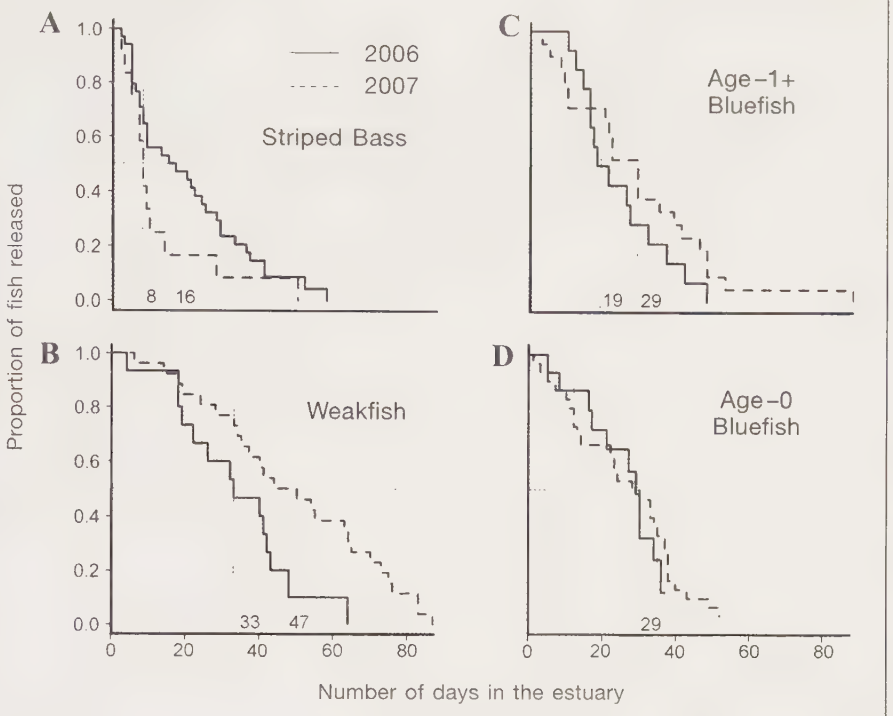

Figure 3

Kaplan-Meier analysis showing that (**A**) tagged Striped Bass (*Morone saxatilis*) used the Navesink River for the fewest number of days, (**B**) Weakfish (*Cynoscion regalis*) for the greatest number of days, and (**C**) age-1+ and (**D**) age-0 Bluefish (*Pomatomus saltatrix*) were resident in the estuary for intermediate durations in 2006 and 2007 for a study of residence times and habitat duration of these 3 predators. Vertical lines crossing the horizontal line at 0.5 indicate the median number days (numbers above *x*-axis) each species used the small estuarine system in each year.

individuals >500 mm TL were released in May and early June. We released age-0 Bluefish >175 mm TL in August and September. Weakfish were available for release from late June to mid-September.

Release date and body size covaried for each age class of each species during at least one year (Table 1). Smaller fishes were generally available for earlier release. However, in 2007, large age-1+ Bluefish and Weakfish were released earlier than smaller individuals.

Patterns of egress

Although most of the tagged fishes remained in the Navesink River until final egress, several individuals of all age classes of tagged species made temporary excursions out of the estuary for a period ≥3 d. More than half of the Striped Bass that we released in 2006 left the estuary temporarily and returned after absences of 3–53 d (n=18; mean excursion [μ]=15.6 d). In 2007, only 25% of the tagged Striped Bass made temporary excursions (n=3, m=15.6 d, max=33 d). Several Striped Bass made 2 or more excursions (n=7, max=6 d). Three fish that left the estuary in June or July 2006 returned in late August or September after absences ≥50 d.

Weakfish and Bluefish showed stronger fidelity to the estuarine tributary than Striped Bass. More than 74% of the Weakfish and age-1+ Bluefish that we released remained in the estuary until final egress. Temporary excursions of these fishes (Bluefish n: 2006=4, 2007=5; Weakfish n: 2006=5, 2007= 6) lasted 2–52 d (μ=~15 d). In 2006, Bluefish and Weakfish left the estuary temporarily during the period of late July–early August when temperatures exceeded 28°C and freshwater discharge was low (Fig. 2). In 2007, age-1+ Bluefish made excursions outside the estuary in late June–early July, and Weakfish made them throughout the summer. Age-0 Bluefish rarely left the tributary before final egress (n: 2006=1, 2007=3; m=10 d; range: 4–19 d).

Duration of estuarine habitat use

The species and size classes remained in the estuary for different lengths of time (χ^2=40.4, df=7, P<0.001;

Table 2

Results from log-rank tests in the Grho family of statistics used to examine differences between "residency curves" derived from Kaplan-Meier survival analysis (χ^2=40.4, df=7, P=1.07e06; see Fig. 3) for fishes tagged with acoustic transmitters and released in the Navesink River, New Jersey, in 2006 and 2007 for a study of residence times and duration of habitat suitability for 3 predators: age-1+ Striped Bass (*Morone saxatilis*), age-0 and age-1+ Bluefish (*Pomatomus saltatrix*), and age-1+ Weakfish (*Cynoscion regalis*). Analysis used year and species-and-age class as predictors. V=Variance.

Species	Year	Number	Observed (O)	Expected (E)	$(O-E)^2/E$	$(OE)^2/V$
Age-0 Bluefish						
	2006	15	11	10.21	0.0606	0.0688
	2007	30	29	25.32	0.5350	0.6775
Age-1+ Bluefish						
	2006	14	14	9.90	1.6978	1.9043
	2007	21	21	22.39	0.0869	0.1109
Striped Bass						
	2006	34	33	21.05	6.7900	8.2661
	2007	12	12	4.41	13.0586	14.1044
Weakfish						
	2006	15	14	16.64	0.4175	0.4900
	2007	26	26	50.08	11.5787	20.9341

Fig. 3, A–D, Tables 1 and 2). Smaller individuals (300–500 mm TL) of all species were more likely to have longer residence times than larger fishes. Striped Bass typically used the system for the fewest number of days. Weakfish had the longest residencies.

Striped Bass used the estuary for a median of 16 d in 2006 and of 8 d in 2007. This difference was not, however, statistically significant because of the small sample size in 2007 (χ^2=2.5, df=1, P=0.1120). All Striped Bass >485 mm TL used the estuary less than 24 d. Many smaller fish had longer residencies (n=24) and some of them (n=4) used the estuary ≥50 d.

Median residency periods for age-1+ Bluefish were 19 d in 2006 and 29 d in 2007, but the interannual difference was not significant (χ^2=1.3, df=1, P=0.248). Several age-1+ Bluefish <500 mm TL (n=8) used the estuary >40 d. Age-0 Bluefish used the system for a median of 29 d, and distributions of residencies were nearly identical in the 2 years of this study (χ^2=0.2, df=1, P= 0.651). Age-0 fish remained in the river for as long as 52 d (n=2). Residencies of tagged age-0 and age-1+ Bluefish were not statistically different (χ^2=1.8, df=3, P= 0.625). However, we were unable to tag age-0 fish <175 mm TL that occurred in the Navesink River as early as June (senior author, unpubl. data), and receivers were removed before the final egress of several tagged age-0 individuals (n: 2006=4, 2007=1). Therefore, age-0 Bluefish probably used the system much longer than age-1+ fish.

Weakfish remained in the estuary for a median of 33 d in 2006 and 47 d in 2007 (χ^2=5.6, df=1, P=0.02). Residencies may have been longer in 2007 because, during that year, Weakfish were released earlier and the observation period was longer. All Weakfish <400 mm TL (n=18) used the estuary ≥40 d and 10 individuals were resident >60 d.

Effects of environmental variables and body size on residence and egress

Smaller individuals of all 3 species tended to remain in the estuary at warmer temperatures than those preferred by larger individuals (Table 3, Fig. 4). Size-dependent temperature responses were continuous for Striped Bass and Weakfish but discontinuous for Bluefish. On average, Striped Bass were more likely to leave the system when temperatures exceeded 23°C than when cooler temperatures occurred (Fig. 4A). However, temperature effects were greater for larger Striped Bass, which left rapidly as temperatures warmed in the early summer. In contrast, smaller fish were more likely to remain in the system into the summer when temperatures were relatively warm. Large Bluefish released in early summer were also likely to emigrate from the estuary when temperatures increased above 23°C (Fig. 4C). In contrast, smaller age-1+ Bluefish were likely to be present when temperatures were warmer (Fig. 4D). Age-0 Bluefish were likely to remain in the estuary when temperatures were warmest. It was unlikely for age-0 Bluefish to leave until autumn temperatures fell below ~20.5°C (Fig. 4E). Weakfish were resident in the estuary at the warmest temperatures and were likely to leave the estuary when temperatures cooled below 23°C (Fig. 4B). Larger Weakfish emigrated at slightly higher temperatures than smaller fish.

All 4 species-and-age classes were more likely to leave the estuary when the Swimming River dis-

Table 3

Results from the final generalized additive mixed models of effects of body size, estuarine temperature, and freshwater discharge (FW) on the residence time of ultrasonically tagged Striped Bass (*Morone saxatilis*), Bluefish (*Pomatomus saltatrix*; age-0 and age-1+), and Weakfish (*Cynoscion regalis*) released into the Navesink River, New Jersey, in 2006 and 2007 (see Figs. 4 and 5 for deviance plots). Individual fish was included as a random effect (i.e., intercept) in all models. Temporal autocorrelation in detections was considered as a first-order, autoregressive process that occurred within each fish. The independent variables included in initial models were *year* as a factor, as well as *release day, body length, temperature*, and *freshwater discharge*, all of which were first considered with cubic smoothing splines (s) with a maximum of 4 degrees of freedom. Tensor product smooths (t2) were used to model interactions. Variables were included as linear effects if expected degrees of freedom (EDF) of splines were close to 1, and they were eliminated from models when they did not contribute to a reduction in Akaike's information criterion (AIC). Body length (total length in millimeters) was considered as a class variable in modeling the temperature response of age-1+ Bluefish because the length× temperature interaction was strongly discontinuous.

Species and Parametric coefficient	Estimate	SE	*Z*-value	*P*-value	AIC
Striped Bass					
Intercept	−2.778	0.177	−15.73	<0.0001	4354
Approximate significance of nonparametric terms	EDF	χ^2			
t2 (*Temperature, body length*)	16.678	228.65		<0.0001	4111
s(log(*FW Discharge* + 1))	3.898	201.90		<0.0001	3888
s(Release day)	2.925	29.66		<0.0001	3844
Coefficient of multiple determination [R^2]=0.15					
Age-1+ Bluefish					
Intercept	−1.739	0.376	−4.626	<0.0001	4301
Year	−1.055	0.473	−2.230	0.0257	4309
Approximate significance of nonparametric terms	EDF	χ^2			
s(*Temperature*):*Length* <500 mm	3.927	286.79		<0.0001	3700
s(*Temperature*):*Length* >500 mm	2.970	193.74		<0.0001	
s(log(*FW Discharge* + 1))	3.893	418.689		<0.0001	3122
s(*Release day*)	1.958	9.362		0.0088	3120
R^2=0.264					
Age-0 Bluefish					
Intercept	0.861	0.550	1.566	0.1170	1974
log(*FW Discharge* + 1)	0.922	0.171	5.385	<0.0001	1900
Approximate significance of nonparametric terms	EDF	χ^2			
s(*Temperature*)	3.345	330.9		<0.0001	1128
R^2=0.235					
Weakfish					
Intercept	−16.980	4.714	−3.602	0.0179	3731
Year	2.484	1.049	2.367	0.0257	3729
Release day	0.079	0.022	3.555	0.0004	3727
Approximate significance of terms	EDF	χ^2			
t2(*Temperature,Body length*)	12.413	580.5		<0.0001	2060
s(log(*FW Discharge* + 1))	3.865	131.0		<0.0001	1932
R^2=0.368					

charge fell below ~2 m^3 s^{-1} than when discharge was higher (Table 3, Fig. 5). This effect was evident when we included year as a factor and when we modeled years separately. As a result, the response to low discharge did not appear to be related to interannual differences in sample size or freshwater discharge. Striped Bass were also likely to leave the tributary during episodes of high freshwater discharge (>50 m^3 s^{-1}; Fig. 5A). Age-0 Bluefish and Weakfish were best modeled with linear discharge terms, indicating that the animals were not likely to leave the estuary during periods when freshwater discharge was high (Fig. 5, B and C).

There were significant differences in patterns of residency among individual fishes (random intercept; Table 3). Furthermore, the year effect was significant in GAMMs for Striped Bass, Weakfish, and age-1+ Bluefish, consistent with descriptions in the previous section, under *Patterns of egress*. Release date was significant in the models for Striped Bass, Weakfish, and age-1+ Bluefish.

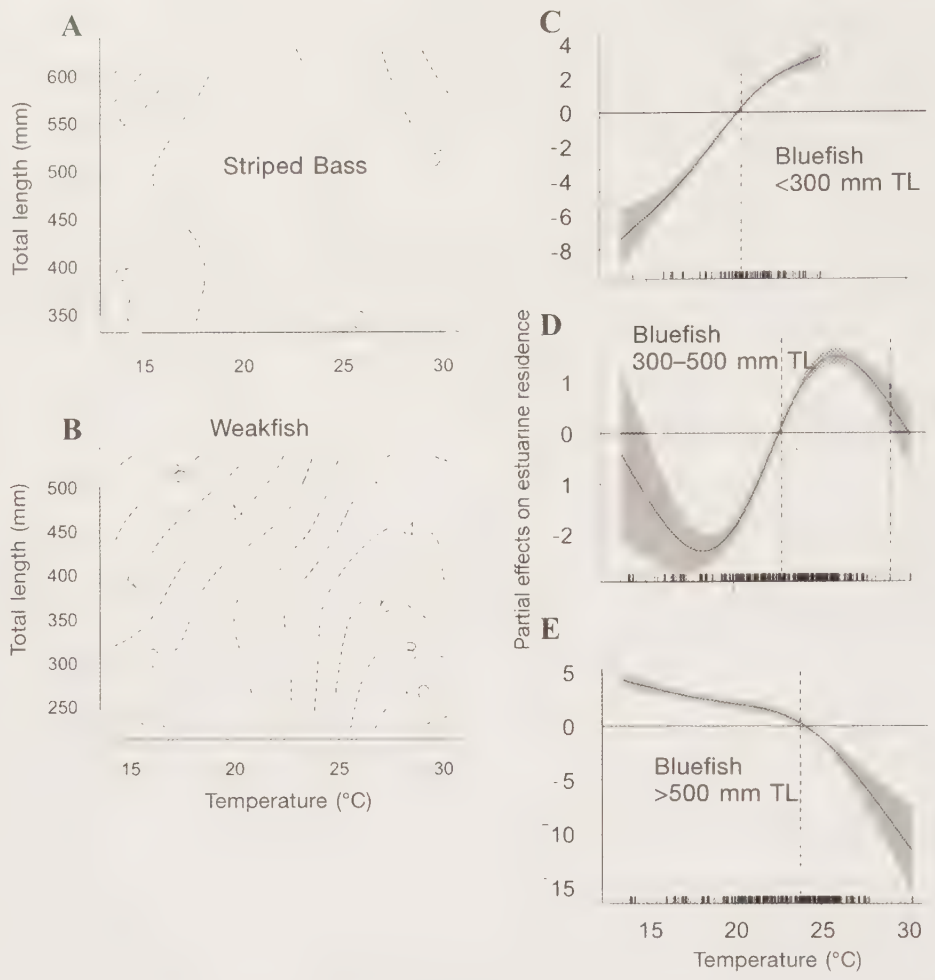

Figure 4

Deviance plots from logistic generalized additive mixed models showing partial effects of temperature and body size on the residence of (**A**) Striped Bass (*Morone saxatilis*) and (**B**) Weakfish (*Cynoscion regalis*), a Bluefish (*Pomatomus saltatrix*) with total lengths (**C**) <300 mm, (**D**) of 300–500 mm, and (**E**) >500 mm, all tagged in the Navesink River in 2006 and 2007 (see Table 3). The relationship of residence to temperature and body size was continuous for Striped Bass and Weakfish which were more likely to be resident over a broader temperature range at smaller body sizes than they were at larger body sizes. Vertical lines crossing the horizontal line at 0.0 indicate boundaries between positive and negative effects, and shaded areas represent ±2 standard-error confidence bands.

The fish that were released later in the season typically were small and generally had longer residencies.

Discussion

Our observations of estuarine residency for individual Striped Bass, Bluefish, and Weakfish indicate that small (~1000 ha), mid-Atlantic estuarine tributaries, such as the Navesink River, contain habitat resources necessary to support survival and adequate growth of age-0 and age-1 individuals for relatively long periods of time during the summer months. Of the age-1+ Striped Bass that we tagged, 25% used the river for more than 26 d, and the same fractions of the Bluefish (age 1 and 0) and age-1+ Weakfish that we tagged used the system for more than 36 and 62 d. Earlier investigations that used fortnightly gillnet surveys of the Navesink River and adjacent Sandy Hook Bay indicated that these 3 predators are abundant in the system, which they use as a feeding habitat, nursery habitat, or both (Scharf et al., 2004; Manderson et al., 2006). Our

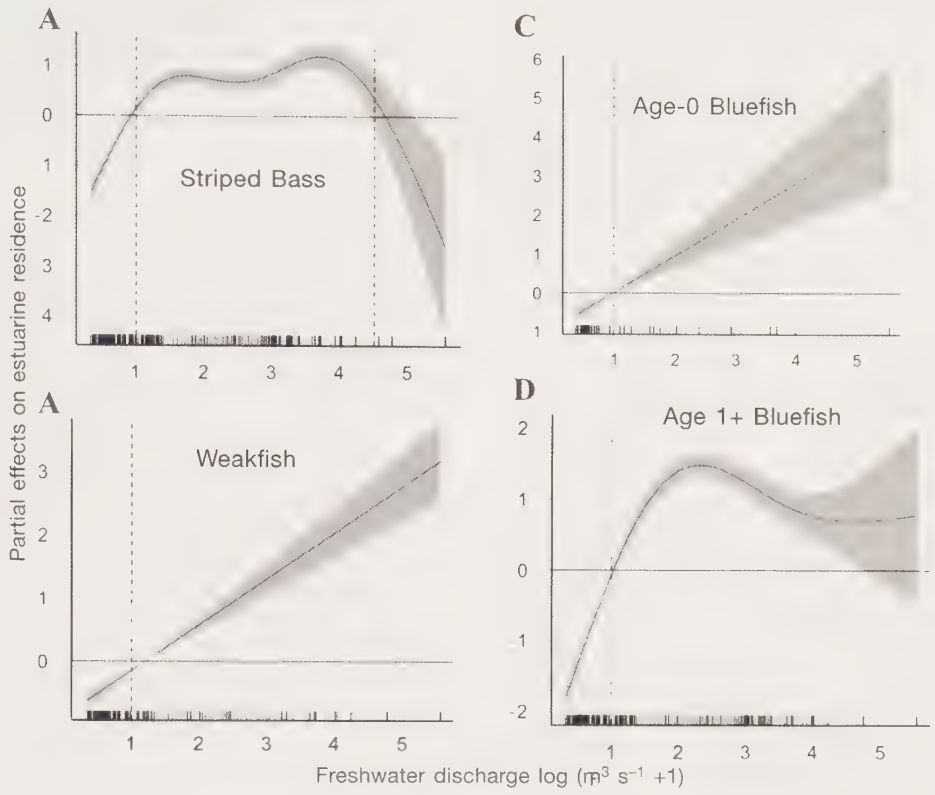

Figure 5

Plots from logistic generalized additive mixed models showing partial deviance effects of freshwater discharge from the Swimming River on the residence of the 3 predator species in the Navesink River (see Table 3) tagged in our study in 2006 and 2007: (**A**) Striped Bass (*Morone saxatilis*), (**B**) Weakfish (*Cynoscion regalis*), and (**C**) age-0+ and (**D**) age-1 Bluefish (*Pomatomus saltatrix*). Vertical lines crossing the horizontal line at 0.0 indicate boundaries between positive and negative effects, and shaded areas represent ±2 standard-error confidence band.

telemetry study indicates that high abundances reflect relatively long-term residence times for predators <500 mm TL rather than a rapid flux of many transient individuals through the ecosystem. Long-term residences of individual fishes with little straying indicates that temperature, oxygen, and prey resources persist at suitable levels in the small tributary for relatively long periods.

Predators with small body sizes had longer residencies and, therefore, appeared to be supported longer by habitat resources in the small ecosystem than were larger individuals. Large Striped Bass and Bluefish (>500 mm TL) used the tributary for a few days to a few weeks during the spring. Large Weakfish (>400 mm TL) released later in the summer were also relatively transient. Smaller age-1+ Bluefish remained in the estuary for intermediate lengths of time. Finally, age-0 Bluefish and small age-1+ Weakfish (<400 mm TL) had the longest residence times (median residence=29 d and ~40 d) that were probably underestimated in our study. Although Weakfish were common in gill nets in May (L. Stehlik and senior author, unpubl. data), we were able to capture them only with hook and line in early July after their diets had shifted from invertebrate to fish prey. Small Bluefish (20–30 mm TL), which cannot be surgically tagged, are collected in Navesink River as early as June in beach seines and fine mesh gillnets (L. Stehlik, unpubl. data). Small Weakfish and Bluefish were, therefore, resident in the Navesink River probably for much longer periods than those that we measured. Our observations of long residences of small predator cohorts in the Navesink River are consistent with observations made in larger estuarine ecosystems (Grothues and Able, 2007; Taylor et al., 2007; Wingate and Secor, 2007; Mather et al., 2009; Turnure, 2010).

The size-dependent patterns of estuarine residence time for the 3 studied predators may have been related to size-dependent requirements for prey resources.

Metabolic rates of animals generally scale with body mass to approximately the ¾ power (Anderson-Teixeira et al., 2009; and references therein; note that in our study we were concerned with resource requirements of individual whole fish that influence residency, not with mass-specific metabolic rates). Therefore, larger or older individuals require more prey resources per unit of energy cost of prey acquisition (i.e., search, capture, handling time, and digestion) than do smaller predators to meet metabolic demand at a given temperature. Prey resources in the Navesink River include large numbers of small invertebrates and fishes, such as age-0 Atlantic Menhaden (*Brevoortia tyrannus*), Atlantic Silverside (*Menidia menidia*), Bay Anchovy (*Anchoa mitchilli*), mysids, and sevenspine bay shrimp (*Crangon septemspinosa*) (Scharf et al., 2004; L. Stehlik and senior author, unpubl. data).

Diet studies of small size classes (<500 mm TL) of predators indicate that age-0 Atlantic Menhaden (<200 mm TL) are preferred prey that, with other small prey, reside in the Navesink River throughout the warmer months. Larger (>200 mm TL), energy rich age-1+ Atlantic Menhaden, consumed by the largest Bluefish and Striped Bass, are abundant in the river during late spring, but they migrate out of the tributary in June and July before returning again in early autumn (Scharf et al., 2004). Early summer egress of the largest Striped Bass and Bluefish (>500 mm TL) from the Navesink River coincided with the typical timing of egress for age-1+ Atlantic Menhaden and other large prey (L. Stehlik and senior author, unpubl. data). These large prey may be required by large fishes, particularly when warm temperatures increase metabolic demand.

Metabolic demand in ectotherms is regulated by environmental temperatures, as well as by body size (Hartman and Brandt, 1995; Brown, 2004; Sousa et al., 2010), and our GAMMs indicated that residence times of the 3 predators in the Navesink River were a function of the interaction between body size and water temperature. For all species, threshold temperatures for egress and breadths of temperatures associated with estuarine residence decreased with increasing body size. The largest age-1+ Striped Bass and Bluefish (>500 mm TL) released in the spring were likely to remain in the river only until temperatures exceeded 23°C in the early summer. Smaller Striped Bass were less sensitive than large fish and remained in the river over a broader range of warmer temperatures. Smaller age-1+ Bluefish were also more likely to be resident at warmer temperatures ranging from 23°C to 26°C. Age-0 Bluefish remained in the estuary at the warmest temperatures recorded and were unlikely to leave until temperatures declined below 19°C during autumn. Finally, Weakfish also remained in the estuary when temperatures were warmest and were more likely to leave the river when temperatures declined below 23°C in the autumn. Smaller Weakfish, however, remained in the river longer and over a broader range of temperatures.

The relationships between estuarine residency time, body size, and environmental temperature that we observed are consistent with bioenergetic studies and metabolic theory (Gillooly et al., 2001; Brown, 2004; Harris et al., 2006; Sousa et al., 2010). The species- and size-specific temperatures of estuarine residence and egress that we measured were extremely similar to temperatures and size-dependent scopes for growth reported by Steinberg (1994) and Hartman and Brandt (1995). In those studies, growth potential exceeded 2% of body weight per day at temperatures of 12–25°C (optimal 15°C) for Striped Bass, 16 –26°C (optimal 20°C) for Bluefish and 20–29°C (optimal 23.5°C) for Weakfish.

Smaller individuals generally had higher optimal temperatures for growth because metabolic demand and prey requirements are generally smaller for animals with small body sizes. For example, the thermal optima for age-1+ Bluefish was ~20°C, but growth potential for age-0 Bluefish reached a maximum at temperatures of ~25–27°C (Steinberg, 1994; Hartman and Brandt, 1995; Scharf et al., 2006). Ranges of optimal temperatures for various performance measures are also generally broader for smaller, juvenile ectotherms (Freitas et al., 2010), and our GAMMs indicated that smaller fishes were more likely than larger fish to remain in the Navesink River over a broader range of temperatures. Because metabolic demand increases with temperature as well as body size, prey supply shortages are more likely to occur during the warmest summer months for large animals in small estuarine tributaries like the Navesink River.

Residence time and egress of the 3 studied predators also were related to the rate of freshwater discharge from the Swimming River into the Navesink River. On the basis of the 4 GAMMs that we constructed independently for the predators, we determined that animals were more likely to leave the small estuarine system when average daily freshwater discharge rates from the Swimming River fell below ~2 m^3 s^{-1} than when discharge rates were higher. High discharge events (>50 m^3 s^{-1}) also appeared to affect residencies of Striped Bass and, perhaps, age-1+ Bluefish. However, in contrast with this low discharge response, high discharge response thresholds varied by species. The predators that we tagged were euryhaline and probably did not respond behaviorally at the scale of the whole estuary to the direct physiological effects of increasing or high salinities. We hypothesize that the effects of low discharge on residence and egress were indirect through hydrographic processes that control the availability of prey resources that support the entire suite of predators that we tagged.

Variability in freshwater discharge is believed to affect estuarine fishes primarily by changing estuarine hydrodynamics that control prey resource availability. Interactions between freshwater discharge and tides control gravitational circulation in estuaries and the advection and concentration of the essential building blocks of estuarine food webs. As a result, estuaries

are traps for autochthonous and allochthonous nutrients and organic matter from adjacent terrestrial and marine systems (MacCready and Geyer, 2010). Stable isotope studies indicate that estuarine food webs are supported by inputs of freshwater and terrestrial sources of nutrients and organic matter (Kostecki et al., 2010). It is assumed that discharge effects on estuarine hydrodynamics and nutrient transport ultimately concentrate high secondary production of zooplankton in estuarine regions where fresher and saltier waters converge (North and Houde, 2006; Baptista et al., 2010). These mechanisms are thought to produce a dome-shaped relationship between estuarine fish production and freshwater discharge (Dolbeth et al., 2010; and references therein).

In the Navesink River, tidal asymmetries produce a short-duration, high-velocity flood tide followed by a long, slow ebb (Chant and Stoner, 2001). During flood tides, particles are suspended and transported upstream. When freshwater discharge from the Swimming River is sufficient, the water column in the Navesink River stratifies during the ebb and particles accumulate in the central and upper reaches of this river. Finer particles and flocculants can remain in suspension in the upper Navesink River (Fig. 1., between locations B and C), where a convergence zone is formed by the turbulent mixing of freshwater inflow from the Swimming River and tidal inflows of saltwater from Sandy Hook Bay and the Atlantic Ocean (Fugate and Chant, 2005).

In this area, Shaheen et al. (2001) reported high concentrations of the copepod *Eurytemora affinis*, an important constituent of estuarine food webs. We measured relatively sharp gradients in salinity and chlorophyll-*a* and, compared with levels observed in other areas in our study, higher abundances of small fish prey, including Atlantic Silverside and age-0 Atlantic Menhaden in combined hydrographic and gillnet surveys (L. Stehlik and senior author, unpubl. data). Additionally, most of the predators that we tagged established home ranges in this region for days to weeks when temperatures in the upper estuary remained below thresholds associated with egress (L. Stehlik and senior author, unpubl. data; see also Scharf et al., 2004; Manderson et al.[2]).

Estuaries change from stratified to well-mixed states when freshwater discharge decreases and salinity stratification weakens to the point that estuarine Richardson numbers reach a range of 0.08–0.8 (Fischer, 1979; MacCready and Geyer, 2010). This transition occurs in the Navesink River when freshwater discharge from the Swimming River falls to ~1 m^3 s^{-1}, (Chant[3]), a discharge rate similar to the value at which all the predators we tagged were likely to leave this small estuary in New Jersey. We speculate that the relationship between predator egress and freshwater discharge reflects a shift from a partially mixed to a fully mixed estuarine state and the relaxation of physical mechanisms that control and concentrate the high primary and secondary productivity that supports the 3 studied predators in the upper reaches of this estuary.

Conclusions

Our analyses of residence time and egress of individual Striped Bass, Bluefish, and Weakfish in the Navesink River, New Jersey, indicate that small estuarine tributaries contain the habitat resources required to sustain juvenile and small adult stages of these 3 predators for relatively long periods of time but that the resources that regulate habitat suitability are ephemeral. Required resources include temperature, which regulates metabolic demand and predatory capacity in cold-blooded fishes (Magnuson et al., 1979; Neill et al., 1994). Summer temperatures in the Navesink River appeared to support smaller predators for longer durations than they did for larger fishes presumably because prey requirements increase with body size and temperature and because the small tributary is dominated by small rather than large prey during the warmest summer months.

Freshwater discharge also appeared to be a critical habitat resource that controlled residence time for animals in this estuary. We believe this relationship reflects the essential role that freshwater discharge plays in regulation of physical processes that both drive and concentrate the secondary productivity required to meet the prey resource requirements of the predators. Other factors that we were not able to measure effectively, particularly dissolved oxygen concentrations and human predation pressure, also may have influenced habitat suitability and the residence time and timing of egress of predators in this small estuarine system (Brady et al., 2009).

Because estuaries occur at the land–sea boundary, high-frequency variability in atmospheric temperature, precipitation, and wind is rapidly translated into variability in water temperature, freshwater discharge, dissolved oxygen, and other biophysical processes that determine estuarine habitat suitability. Changes in seasonal rates of warming, cooling, and precipitation that alter and reduce the persistence of suitable estuarine habitats should require animals to undertake more frequent, long-distance movements that are energetically costly. Conversely, long durations of suitable habitat conditions require fewer shifts in local home range (Martinho et al., 2009) and allow the allocation of resources to the life-history processes of growth and reproduction instead of long-distance movements.

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Increased movement costs should come at the expense of strategies that reduce predation risk and increase growth and reproduction rates. Changes in atmospheric forcing with climate change are coherent over spatial scales of 1000s of kilometers (Hare and Able, 2007; Manderson, 2008; Shearman and Lentz, 2010). As a result, climate-driven changes in habitat and persistence should affect the energy budgets and survival of many individuals over broad areas. These effects should be translated across a level of ecological organization to affect the birth and death rates of regional fish populations.

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Effects of fluctuations in sea-surface temperature on the occurrence of small cetaceans off Southern California

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Abstract—The link between ocean temperature and spatial and temporal distribution patterns of 8 species of small cetaceans off Southern California was examined during the period 1979–2009. Averages and anomalies of sea-surface temperatures (SSTs) were used as proxies for SST fluctuations on 3 temporal scales: seasonal, El Niño–Southern Oscillations (ENSO), and Pacific Decadal Oscillations (PDO). The hypothesis that cetacean species assemblages and habitat associations in southern California waters co-vary with these periodic changes in SST was tested by using generalized additive models. Seasonal SST averages were included as a predictor in the models for Dall's porpoise (*Phocoenoides dalli*), and common dolphins (*Delphinus* spp.), northern right whale dolphin (*Lissodelphis borealis*), and Risso's dolphin (*Grampus griseus*). The ENSO index was included as a predictor for northern right whale, long-beaked common (*Delphinus capensis*), and Risso's dolphins. The PDO index was selected as a predictor for Dall's porpoise and Pacific white-sided (*Lagenorhynchus obliquidens*), common, and bottlenose (*Tursiops truncatus*) dolphins. A metric of bathymetric depth was included in every model, and seafloor slope was included in 5 of the 9 models, an indication of a distinctive spatial distribution for each species that may represent niche or resource partitioning in a region where multiple species have overlapping ranges. Temporal changes in distribution are likely a response to changes in prey abundance or dispersion, and these patterns associated with SST variation may foreshadow future, more permanent shifts in distribution range that are due to global climate change.

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Cetaceans are higher-trophic-level marine predators whose movement patterns and habitat preferences are typically related to the distribution of their prey (Wishner et al., 1995; Gowans et al. 2007). Unlike baleen whales, small cetaceans (porpoises, dolphins, and small-toothed whales) generally do not undertake ocean-scale annual migrations to track prey or to move between breeding and feeding grounds. Rather, small cetaceans may display a high degree of site fidelity, or they may move seasonally inshore and offshore or along regional-scale coastlines (Leatherwood et al., 1984; Dohl et al., 1986; Shane et al., 1986; Forney and Barlow, 1998).

Although many small cetacean species may overlap in any one region of their total range, they often differ in their occurrence or habitat-use patterns, perhaps reflecting competitive exclusion or niche partitioning. This separation of habitat and resources often occurs along depth, slope, and sea-surface temperature (SST) gradients (Reilly, 1990; Forney, 2000; Ballance et al., 2006; MacLeod et al., 2008). Habitat preferences likely reflect differences in preferred prey. Dolphins may follow prey habitats as they shift not only seasonally but through large-scale climate-driven changes such as the El Niño–Southern Oscillation (ENSO) or the Pacific Decadal Oscillation (PDO) (Shane, 1995; Defran, 1999; Benson et al., 2002; Ballance et al., 2006).

We examined the distribution and relative abundance of multiple species of small cetaceans across shifting temperature regimes off South-

ern California by using a unique coupled cetacean-oceanographic long-term data set. This data set enables a rare opportunity to assess interdecadal changes in cetacean distribution over a broad spatial extent. The co-occurrence of cold- and warm-water cetacean species makes this location an ideal one at which to examine potential effects of climate variation on regional distribution patterns at different temporal scales (intra-annual, annual, and decadal).

The Southern California region represents the convergence of warm- and cold-water masses and supports populations of both warm- and cold-water, small cetacean species (Forney and Barlow, 1998). During the summer, the cold, equatorward flowing California Current system has a seasonal maximum (7.8 Sverdrups [Sv], ~7.8 million m^3 s^{-1}). The California Current turns shoreward (poleward) at approximately 32°N and becomes the California Countercurrent. The California Countercurrent and California Undercurrent also have a seasonal maximum in late summer and into the fall and, therefore, dominate the Southern California Bight, with a combined maximum transport in October of 1.8 Sv. The California Undercurrent reaches its minimum (0.8 Sv) and turns equatorward in the spring. The California Countercurrent turns equatorward then as well; therefore, all flow through the Southern California region becomes equatorward in the spring, allowing the California Current to dominate and transport cooler water farther south (Hickey, 1993; Hickey et al., 2003).

In the California Current system, strong El Niño years in the positive ENSO phase have been linked to increased downwelling, warmer SSTs, and a deepening of the thermocline observed off Southern California (Sette and Isaacs, 1960; McGowan, 1985; Caldeira et al., 2005). During the warm, positive phase of the PDO, the California Current is weakened and the Countercurrent is strengthened. This intensified current brings warmer waters farther north and west into and beyond the Southern California region, creating warm SST anomalies along the California coast. In contrast, during the cool, negative PDO phase, the California Current is stronger, bringing cool water farther south and east into the region (Mantua and Hare, 2002). A PDO regime shift from cool to warm occurred around 1977, before our study, and a shift back to a cool PDO may have occurred during the last decade starting in 1998–99 (Peterson and Schwing, 2003; Zhang and McPhaden, 2006; Wang et al., 2010).

Two long-term sets of ship-based surveys have been conducted in Southern California waters, making it an ideal region for this investigation. The California Cooperative Oceanic Fisheries Investigations (CalCOFI) has been conducting quarterly cruises that have sampled a breadth of oceanographic and lower-trophic-level biological data since 1949. Marine bird and mammal observations were added in 1987 (Hyrenbach and Veit, 2003; Sydeman, et al., in press). The NOAA Southwest Fisheries Science Center (SWFSC) also regularly has conducted marine mammal abundance surveys that have included this region since 1979.

Changes in SST have been linked to changes in all levels of the food web, from immediate phyto- and zooplankton responses to lagged alterations in numbers, diet, and even reproductive success of higher-level organisms, such as fishes, seabirds, and marine mammals (Tibby, 1937; Hubbs, 1948; McGowan, 1985; McGowan et al., 2003; Sydeman et al., in press). It follows that small cetacean populations would respond to such variations in SST, likely as a response to changes in prey populations, as has been shown for seabirds (Hyrenbach and Veit, 2003). In addition, population-level responses to these fluctuations in temperature may predict their reaction to future ocean conditions as global ocean temperatures rise.

We investigated such responses by 8 species of small cetaceans across 30 years, using SST averages and anomaly indices as a proxy for environmental variation on 3 temporal scales: seasonal (yearly), ENSO (2–7 years) and PDO (~30 years). We predicted that patterns in small cetacean occurrence and distribution within Southern California waters would follow similar trends reported for seabirds (Hyrenbach and Veit, 2003; Yen et al., 2006; Sydeman et al., in press) and other cetaceans (Forney and Barlow, 1998; Becker et al., 2012). For small cetaceans off Southern California, the following trends were predicted: 1) species assemblages will differ depending on the dominant SST regime, 2) cold-water–associated species will be more abundant and broadly distributed when cold-water conditions prevail, 3) warm-water–associated species will dominate during warm-water conditions, and 4) the latter 2 patterns will be compounded when SST fluctuations co-occur on multiple scales.

Materials and methods

Study area and survey methods

Our study area was situated between 117°W and 125°W longitude and from 30°N to 35°N latitude (Fig. 1) and includes the Southern California Bight as well as deeper offshore waters. The Southern California Bight is a region of complex bathymetric features, including the Channel Islands and a series of deep basins and shallow ridges (Dailey et al., 1993). Beyond the steep 2000-m slope lies the ocean basin, with a mean depth of >3500 m. Three regions, associated with depth, were defined in the analyses for this study (Fig. 1): 1) the inshore and island region (with a mean depth <1100 m and a maximum depth <2000 m; 2) the slope region (with a mean depth of 1000–3200 m and a depth range of 500–3500 m); and the offshore region (with a mean depth >3500 m and a maximum depth >4000 m). The terms for these three regions will be used throughout the study.

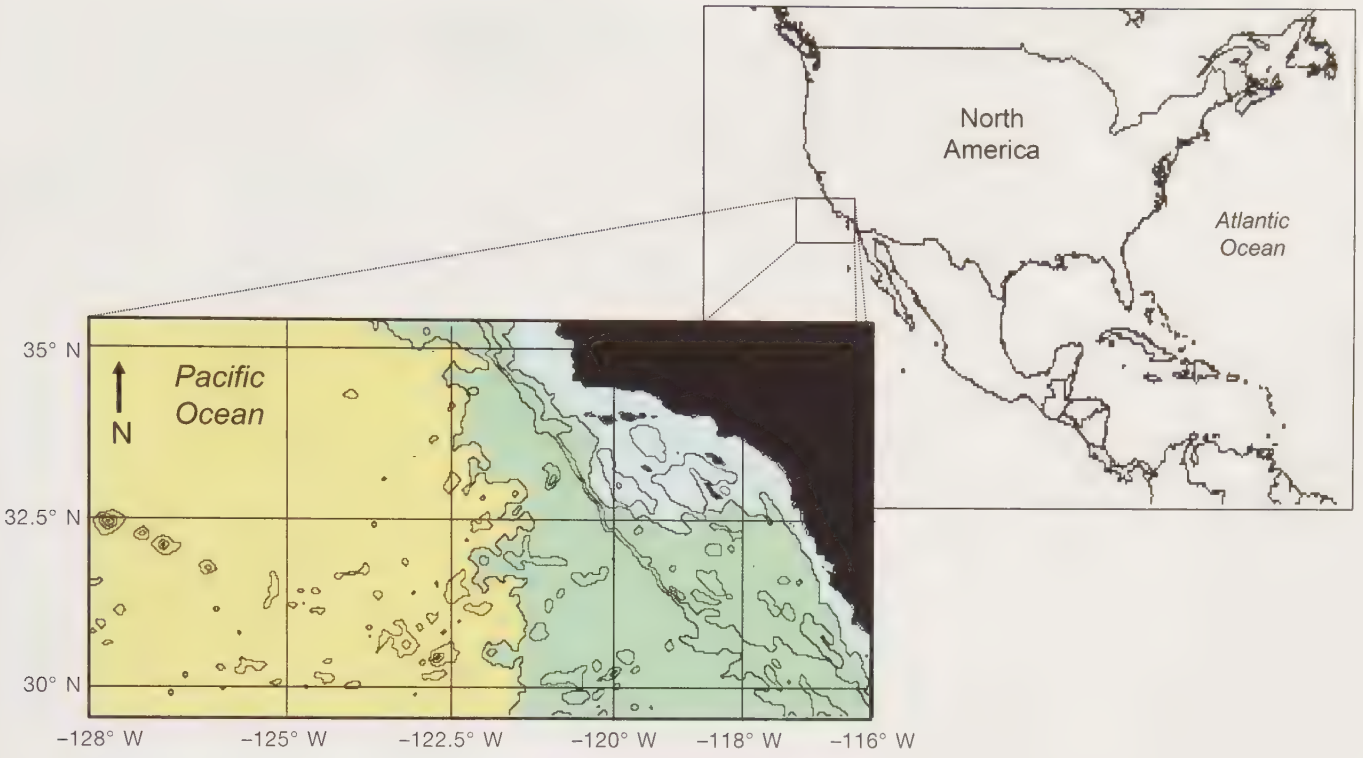

Figure 1

Map of the study area located off Southern California in the eastern North Pacific Ocean, south of Point Conception and incorporating the Channel Islands, in which small cetacean distributions were recorded during 1979–2009. Colored areas indicate 500-m depth contours. The blue area (mean depth <1100 m, maximum depth <2000 m) was considered the inshore and island region, the green area (mean depth of 1000–3200 m, within a depth range of 500–3500 m) was considered the slope region, and the yellow area (mean depth >3500 m, maximum depth >4000 m) was considered the offshore region.

We analyzed data from visual sightings of marine mammals from 105 separate survey cruises conducted by both CalCOFI and SWFSC from 1979 to 2009 (Fig. 2). During CalCOFI cruises from May 1987 to April 2004 (CalCOFIa) marine mammals were recorded as part of standardized CalCOFI top predator surveys that were focused primarily on marine birds. The strip-transect methods of Tasker et al. (1984) were followed. Observations were made with the naked eye by a single observer stationed on one side of the flying bridge or outside the main bridge. Marine mammals were recorded only if they occurred within the 300-m strip transect used for birds or within 1000 m of the vessel for large cetaceans. Each CalCOFI transect line extended from directly in front of the ship to 90° on the observation side. Group sightings of marine birds and mammals were summarized into 3-km bins, with the latitude and longitude determined for the centroid of each bin. Additional details of field methods are provided in Veit et al. (1996; 1997), Hyrenbach and Veit (2003), and Yen et al. (2006).

In July 2004, 2 dedicated marine mammal visual observers were added to the CalCOFI cruises (CalCOFIb), and a standard line-transect protocol replaced the strip-transect protocol (Burnham et al., 1980; Buckland et al., 2001). A complete description of survey methods can be found in Soldevilla et al. (2006). Each observer monitored a 90° field of view from bow to abeam, one on each side of the ship, and alternated between scanning with Fujinon[1] 7×50 binoculars (Fujifilm Corp., Tokyo) and with the naked eye. Survey effort was calculated on the basis of latitude and longitude at the start and end of each trackline.

For all CalCOFI surveys, observations were made on daytime tracklines between stations, and no visual observation effort was conducted while the vessel was stationary. All visual effort was conducted in sea state conditions rated 5 or less on the Beaufort scale. Data used for analyses were generally from 4 surveys per year from 1987 to 2009, 1 survey per season (typically in the same month but with some variation). In 5 of these years, only 3 surveys were conducted. In 1998, surveys were carried out monthly to capture a time series of oceanographic measures in a strong El Niño year. However, to be consistent across all years for purposes of analysis, these cruise data were combined into

[1] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

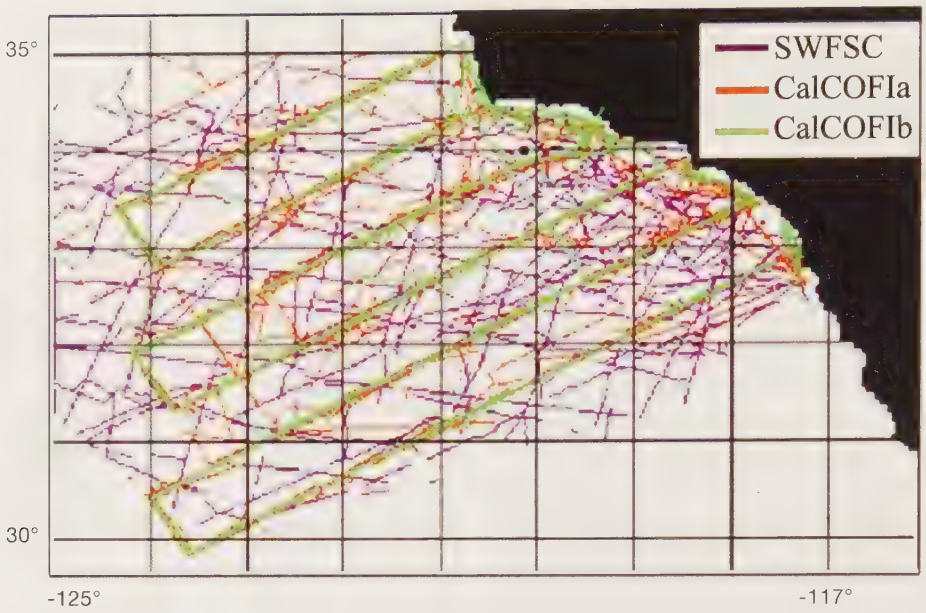

Figure 2

Transect lines surveyed for all studies of small cetaceans off Southern California in 1979–2009. Orange lines indicate surveys conducted during California Cooperative Oceanic Fisheries Investigations (CC) cruises from 1987 to 2004, green lines indicate CC surveys conducted from 2004 to 2009, and purple lines indicate surveys conducted by the NOAA Southwest Fisheries Science Center (SWFSC) from 1979 to 2009. Black lines indicate latitude and longitude in 1° increments, which were used to create the grid sections for analyses in the generalized additive models.

4 quarters (winter, spring, summer, and fall; see the next section, *Environmental data*, for details). A full summary of surveys, along with total effort (in kilometers) and sightings per year for all species is provided in Appendix I.

Data for analyses also came from 10 different SWFSC cruises, conducted primarily in the summer and fall (from July through November) from 1979 through 2005 and covering an area that included Southern California waters (Appendix I). For SWFSC cruises, standard line-transect protocols were followed, as described in Barlow and Forney (2007) and Kinzey et al.[2] The latter cruises had 3 observers on the flying bridge, 2 of whom used "big eye" 25×150 binoculars to scan 90° from bow to abeam on either side of the flying bridge. The third observer monitored the entire forward 180° with 7×50 binoculars and the naked eye. Survey effort (in kilometers) was calculated either from the latitude and longitude positions at the start and end of each trackline (1979–84 surveys) or from latitude and longitude positions recorded approximately every 10 min along the track (1991–2005 surveys).

Eight species of small cetaceans were examined in this analysis. The 3 warm-temperate and tropical species were short-beaked common dolphin (*Delphinus delphis*), long-beaked common dolphin (*D. capensis*), and striped dolphin (*Stenella coeruleoalba*). The 3 cold-temperate species were Pacific white-sided dolphin (*Lagenorhynchus obliquidens*), northern right whale dolphin (*Lissodelphis borealis*), and Dall's porpoise (*Phocoenoides dalli*). The remaining 2 species were considered cosmopolitan, distributed globally in tropical and temperate waters: Risso's dolphin (*Grampus griseus*) and bottlenose dolphin (*Tursiops truncatus*) (Reeves et al., 2002).

All bottlenose dolphin sightings in this study were presumed to be offshore animals because most coastal animals remain within about 1 km from the shore (Hanson and Defran, 1993) and surveys were conducted at least 5–10 km from the coast. In addition to their individual species' models, short- and long-beaked common dolphins were combined into an additional *Delphinus* species category because the 2 species were not recognized formally as distinct until 1994 (Heyning and Perrin, 1994). Furthermore, they were not distinguished on SWFSC cruises before 1991 or on CalCOFI cruises before August 2004. Therefore, the data sets for long-beaked and short-beaked common dolphin are smaller than the data sets for all other species, and the data set for *Delphinus* spp. consists of all combined common dolphin sightings from all cruises.

[2] Kinzey, D., P. Olson, and T. Gerrodette. 2000. Marine mammal data collection procedures on research ship line-transect surveys by the Southwest Fisheries Science Center. NOAA Southwest Fisheries Science Center, Admin. Rep. LJ-00-08, 32 p.

Environmental data

Three variables were used to represent variations in SST on different temporal scales: quarterly SST averages, ENSO indices, and PDO indices. Monthly averaged SST data from 1985 to 2009 were from NOAA Advanced Very High Resolution Radiometer (AVHRR) Pathfinder satellite data, which have a spatial resolution of ~4.1-km (http://www.nodc.noaa.gov/SatelliteData/pathfinder4km). For 1981–84, NOAA AVHRR data (multichannel averaged SST with a 5.7-km resolution) were also used. No satellite data were available before 1981; therefore, a missing data filter and a single imputation method were used to create values for 1979 and 1980 with the mean of the SSTs for the other years (Hastie, 1991; Nakagawa et al., 2001).

With Windows Image Manager, vers. 6 (WimSoft, San Diego, CA), seasonal SST averages were calculated from the monthly SST data. These SST averages were estimated for each quarter and each grid cell (see the following paragraph) for the period 1979–2009 (spring: February–April; summer: May–July; fall: August–October; winter: November–January). NOAA ENSO anomaly data, derived from the Oceanic Niño Index as a 3-month running mean of SST anomalies from 1971 to 2009 in the Niño 3.4 region (http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml), were used as a proxy for ENSO for 1979–2009. The Niño 3.4 region is centered on the equator; therefore, the index indicates the relative strength of the ENSO event rather than SST anomaly values for Southern California waters. PDO anomaly data, averaged for the period from 1900 to 2009, from the University of Washington (http://jisao.washington.edu/pdo) were used as a proxy for the PDO regime from 1979 to 2009. The PDO index is derived from a monthly averaged SST for North Pacific waters poleward of 20°N.

Depth data were taken from the NOAA National Geophysical Data Center's ETOPO2 2-min global relief database (http://www.ngdc.noaa.gov/mgg/fliers/06mgg01.html). The study area was divided into 52 grid cells of 1° (111 km or 60 nmi) latitude by 1° longitude, leading to grid cell areas that ranged from 2940 to 3120 km^2. The gridded depth data were then assigned to each of the grid cells, and minimum, maximum, and mean depth values were calculated for each grid cell, along with the maximum seafloor slope per cell. These large grid cells correspond to approximately one day of effort for each of the surveys and were designed to be large enough to smooth out the mesoscale features that occur on shorter temporal and spatial scales than were of interest here. Although mesoscale features, such as fronts or eddies, are often observed to be hotspots for marine mammals, the multidecadal data set used in our study allowed for a synoptic examination of changing distribution patterns throughout the study area.

Modeling cetacean sighting rates

Generalized additive models (GAMs) of species sighting rates as a function of the temperature data and depth values were created with the mixed GAM computational vehicle (mgcv) package in R software, vers. 2.14.2 (R Core Team, 2012) (Hastie and Tibshirani, 1990; Wood, 2006). GAMs use a link function to relate the predictor variables to the mean of the response variable. GAMs also allow nonparametric functions to be fitted to the predictor variables through the use of a smoothing function to describe the relationship between the predictor and the response variables (Hastie and Tibshirani, 1990).

For model development, the grid cells described previously were used as data units, and all effort, sighting, and seasonal SST data were calculated for each cell. This approach allowed for the normalization of spatial and temporal differences in survey data. The type of survey was included as a categorical variable to account for differences in sighting rates due to survey method and platform. For example, because many vessels of different heights were used and heights for some vessels were not reported, standardization of observations for platform heights was not possible. Survey types included SWFSC (1979–2005), CalCOFIa (1987–2004), and CalCOFIb (2004–09). For each survey type, the number of group sightings of each species within each 1° cell, standardized by the log of the amount of effort per cruise (in kilometers), was modeled by assuming a Poisson distribution with a log link function.

Potential predictor variables in the model were the following: seasonal SST averages of each grid section (SeasAv); ENSO index (ENSO); PDO index (PDO); the mean (DepthMean), minimum (DepthMin), and maximum (DepthMax) depth (in meters) for each grid section; the maximum slope for each grid section (Slope); and the quarter (Quarter) as a categorical variable for identification of interannual patterns. Although sea state has been shown to be an important predictor of sighting rates in other cetacean habitat and trend models (Becker, 2007), the condition of the sea surface was not recorded in early CalCOFI observations and, therefore, sea state was not included in this analysis. Instead, only data recorded when the sea state was rated 0–3 on the Beaufort scale during SWFSC cruises and later CalCOFI cruises were used to standardize for differences in survey effort and, thus, make the different platforms as comparable as possible.

We used the number of group sightings, rather than the number of individuals, as our measure of relative encounter rate, essentially creating encounter rate models of group sightings per unit (kilometer) of survey effort (SPUE) (Bordino et al., 1999; Stockin, 2008). A correlation analysis of annual rates of group sightings in relation to mean group size per year

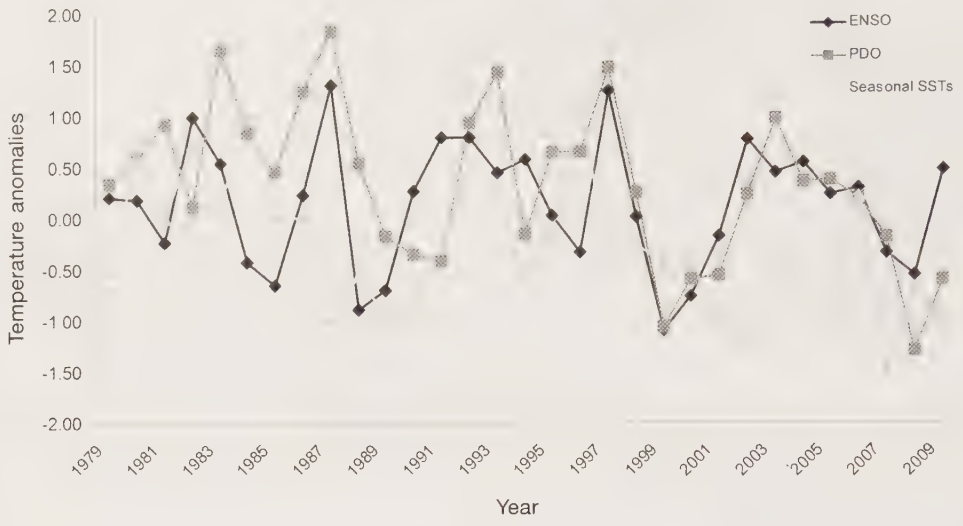

Figure 3

El Niño–Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO) sea-surface temperature (SST) anomalies in 1979–2009 and seasonal SST anomalies from Southern California waters from 1981 to 2009. PDO SST anomalies were calculated with data collected in 1900–2009, and ENSO anomalies were calculated with a 3-month running mean for the period 1950–2009. Seasonal SST anomalies were calculated from the SST averages obtained through the use of NOAA Advanced Very High Resolution Radiometer (AVHRR) Pathfinder satellite data and averaged per quarter.

also was conducted to determine whether group size correlated with the number of groups encountered.

To select predictor variables for inclusion in each model, a likelihood-based smoothness selection method, instead of a traditional stepwise method, was applied with the restricted maximum likelihood (REML) criterion (Patterson and Thompson, 1971; Wood, 2006). Each predictor variable was tested for inclusion in the model with a tensor product approach coupled with a smoothing function defined by a cubic regression spline with shrinkage. The best model was selected on the basis of a combination of the information-theoretic descriptor Akaike's information criterion (AIC; Akaike, 1976) and REML. Next, an interactive term selection method was applied to sequentially drop the single term with the highest nonsignificant *P*-value and then refit the model until all terms were significant. The best-fit model was therefore one that minimized AIC and maximized REML and the explained deviance and that included only significant predictor variables. In addition, the ENSO, PDO, and seasonal SST averages, as well as each of the depth metrics, were tested for correlation if more than one of them was included in a model as a significant predictor. These variables were then included together only if they were not correlated. If the variables were correlated, then only the most significant variable remained in the final model.

Results

Sea-surface temperature for the study area over the period 1979–2009 ranged from 12.7°C to 19.4°C, with a mean of 16.2°C. Overall averaged seasonal anomalies ranged from −1.5°C to 1.1°C around the mean (Fig. 3). In comparison, seasonal anomalies by grid section ranged from −3.8°C to 3.4°C. Years with a strong positive PDO (index>1) were 1983, 1987, 1993, 1997, and 2003, and a strong negative PDO (index<−1) occurred in 1999 and 2008 (Fig. 3). Strong positive ENSO years were 1982–83, 1987–88, 1991–92, 1997–98, and 2002–03, and strong negative ENSO years were 1988–89 and 1999–2000 (Fig. 3). No long-term trends in SST were apparent in our data given the levels of seasonal and ENSO variation observed. However, a linear regression of PDO anomaly data shows an overall negative trend in the last 30 years: coefficient of multiple determination (R^2)=0.215, P=0.009. This pattern is likely a result of the PDO regime switch in the last decade (Overland et al., 2008; Hodgkins, 2009).

The correlation analysis revealed that annual sighting rates and mean group size were not correlated for any of the species examined. This finding indicates that, although species may be encountered with varying frequency across years, the number of individual animals per group does not change in a correlated way. For example, if more groups of a given species were

Table 1

The final best-fit generalized additive models are presented here for each of the 8 species of small cetaceans investigated for this study in Southern California waters in 1979–2009. Also included are the restricted maximum likelihood (REML) score, explained deviance (Expl. dev.), and residual degrees of freedom (df) for each model. See Appendix 2 for the *P*-values of each variable in these models. The 8 species were the short-beaked common dolphin (*Delphinus delphis*), long-beaked common dolphin (*D. capensis*), Risso's dolphin (*Grampus griseus*), northern right whale dolphin (*Lissodelphis borealis*), Pacific white-sided dolphin (*Lagenorhynchus obliquidens*), Dall's porpoise (*Phocoenoides dalli*), striped dolphin (*Stenella coeruleoalba*), and bottlenose dolphin (*Tursiops truncatus*); a third model for common dolphins incorporated data for both the short- and long-beaked common dolphins. Variable abbreviations: DepthMin=minimum depth (m), DepthMean=mean depth (m), MaxDepth=maximum depth (m), SeasAv=seasonal averaged sea-surface temperature, ENSO=El Niño–Southern Oscillation, and PDO=Pacific Decadal Oscillation.

Species	Final model	REML	Expl. dev.	Residual df
Short-beaked common dolphin	Quarter + Slope + DepthMean + SeasAv	754.0	23.9%	642
Long-beaked common dolphin	Quarter + DepthMax + ENSO + SeasAv	211.7	57.4%	652
Both common dolphins	Quarter + SurveyType + Slope + DepthMax + PDO + SeasAv	2751.8	32.5%	2415
Risso's dolphin	Quarter + SurveyType + Slope + DepthMean + ENSO + SeasAv	644.7	36.6%	2421
Northern right whale dolphin	SurveyType + DepthMax + ENSO + SeasAv	270.3	26.1%	2428
Pacific white-sided dolphin	Quarter + SurveyType + Slope + DepthMean + PDO	706.2	21.2%	2419
Dall's porpoise	Quarter + SurveyType + Slope + DepthMean + PDO + SeasAv	726.8	27.5%	2423
Striped dolphin	SurveyType + DepthMin	88.3	41.8%	2437
Bottlenose dolphin	SurveyType + Slope + DepthMean + PDO	376.0	46.4%	2429

encountered in a year, the group size would not necessarily also increase or decrease.

The best-fit models are shown in Table 1. Values for explained deviance ranged between 21.2% and 57.4% across species. A summary of group sighting rates is given in Table 2. Six of the 9 models included the Quarter variable, indicating intra-annual variation in the SPUE for each species. Of the 9 models, 7 models included the SurveyType variable; the 1987–2004 CalCOFI cruises ranked lowest and the SWFSC cruises ranked highest in sighting numbers for most species. Of the 9 models, 6 models included the seasonal SST average variable, and 7 models also included either the PDO or ENSO index. The latter results indicate the importance of those temperature fluctuations on small cetacean distribution. All models also included at least one depth metric, previously shown to be an important predictor variable for Southern California cetaceans (e.g., Becker, 2007). Finally, 5 of the 9 models included slope as a predictor.

Common dolphins

Three different models were used for common dolphins: both species of common dolphin in a single combined category, short-beaked common dolphin, and long-beaked common dolphin. The similarities in the model results for both common dolphins and the short-beaked common dolphin indicate that the data for the combined category likely are dominated by sightings of short-beaked common dolphins. Common dolphins were associated with seasonal SSTs of about 14–18°C in all 3 models, indicating possible avoidance of extremely warm or cold temperatures (Fig. 4). For all common dolphin groups, most sightings occurred in the summer and fall, and generally the fewest sightings occurred in the spring. Depth was an important predictor of common dolphin distribution in all 3 models, and slope was included in the models for the combined category and the short-beaked common dolphin. Long-beaked common dolphins were found almost exclusively inshore, and sightings of short-beaked common dolphins and dolphins in the combined group were recorded both inshore and offshore in areas with shallow slopes. The model for both common dolphins combined showed a very slight increase in sightings with negative PDO anomalies, although the overall response was fairly flat (Fig. 4).

Table 2

Summary of sightings, including the number of cruises conducted by the California Cooperative Oceanic Fisheries Investigations and the NOAA Southwest Fisheries Science Center in which each species was encountered and the total number of groups sighted in 1979–2009 in Southern California waters for each studied species of small cetacean: short-beaked common dolphin (*Delphinus delphis*), long-beaked common dolphin (*D. capensis*), Risso's dolphin (*Grampus griseus*), northern right whale dolphin (*Lissodelphis borealis*), Pacific white-sided dolphin (*Lagenorhynchus obliquidens*), Dall's porpoise (*Phocoenoides dalli*), striped dolphin (*Stenella coeruleoalba*), and bottlenose dolphin (*Tursiops truncatus*). Because the short- and long-beaked common dolphins were not recognized formally as distinct until 1994, data for both species were used in a combined category in analyses.

Species	Number of cruises	Number of groups
Short-beaked common dolphin	29	387
Long-beaked common dolphin	22	93
Both common dolphins	105	1537
Risso's dolphin	74	227
Northern right whale dolphin	32	71
Pacific white-sided dolphin	62	217
Dall's porpoise	64	240
Striped dolphin	22	28
Bottlenose dolphin	50	180

Risso's dolphin

Risso's dolphins were largely observed inshore, although they were occasionally observed offshore and in areas of shallow depths and steep slope, as shown in the partial residuals plots for depth and slope (Fig. 5). Sightings peaked slightly during warmer seasonal SSTs, around 18°C, but occurred least frequently in the summer. ENSO also was included in the model and indicated slightly more sightings during positive ENSO phases.

Striped dolphin

Striped dolphins are a tropical and warm-temperate species associated with warm water masses, and dolphins of this species were predominantly observed offshore of the 2000-m depth contour with a deep minimum depth (Fig. 5). Because of this strong offshore distribution, only 28 groups were sighted during 22 cruises. This low number of sightings is in part due to the limitation of including only sightings made in sea states rated 3 or less on the Beaufort scale; because most striped dolphin sightings occurred offshore, many were made in higher-rated sea states and were, therefore, not included. Because of that exclusion, most sightings included for analyses came from data collected during later SWFSC (1991–2005) cruises, making Survey Type an important predictor variable.

Bottlenose dolphin

Bottlenose dolphin groups tended to display a strong inshore and island association. They generally were sighted over the continental shelf, although they were occasionally observed farther offshore, as shown in the depth residuals plots (Fig. 5). The PDO variable was significant, indicating that a slight increase in sightings occurred with negative PDO anomalies.

Northern right whale dolphin

Northern right whale dolphin is 1 of 3 cold-temperate species strongly associated with the California Current system. Therefore, the extent of this species into the Southern California study area was expected to correlate with cold-water intrusions. Sightings were associated with cool SSTs as expected. However, sightings were associated also with both positive and negative ENSO anomalies. Groups of northern right whale dolphins showed a strong association with the slope region, with most sightings located at depths between 2000 and 4000 m, as shown in the depth residuals plot (Fig. 6).

Dall's porpoise

Sightings of Dall's porpoise, another cold-temperate species, peaked during the spring, fall, and winter (Fig. 6), and groups of Dall's porpoises were associated with cool SSTs. However, they were associated with slightly positive PDO phases, as well. They were distributed inshore and offshore, in areas of slightly shallower slopes, as shown in the depth and slope residuals plots.

Pacific white-sided dolphin

Results were unexpected for Pacific white-sided dolphin, the final cold-temperate species the sighting rates of which were anticipated to increase in cooler temperatures. Sightings peaked slightly during the spring quarter when the water temperature was cooler. However, they also exhibited an association with slightly positive PDO indices (Fig. 6). This species was distributed largely inshore, as shown in the depth residuals plot.

Discussion

Patterns of seasonal sea-surface temperatures

Patterns of encounter rate related to seasonal SSTs were largely consistent with past studies within this region

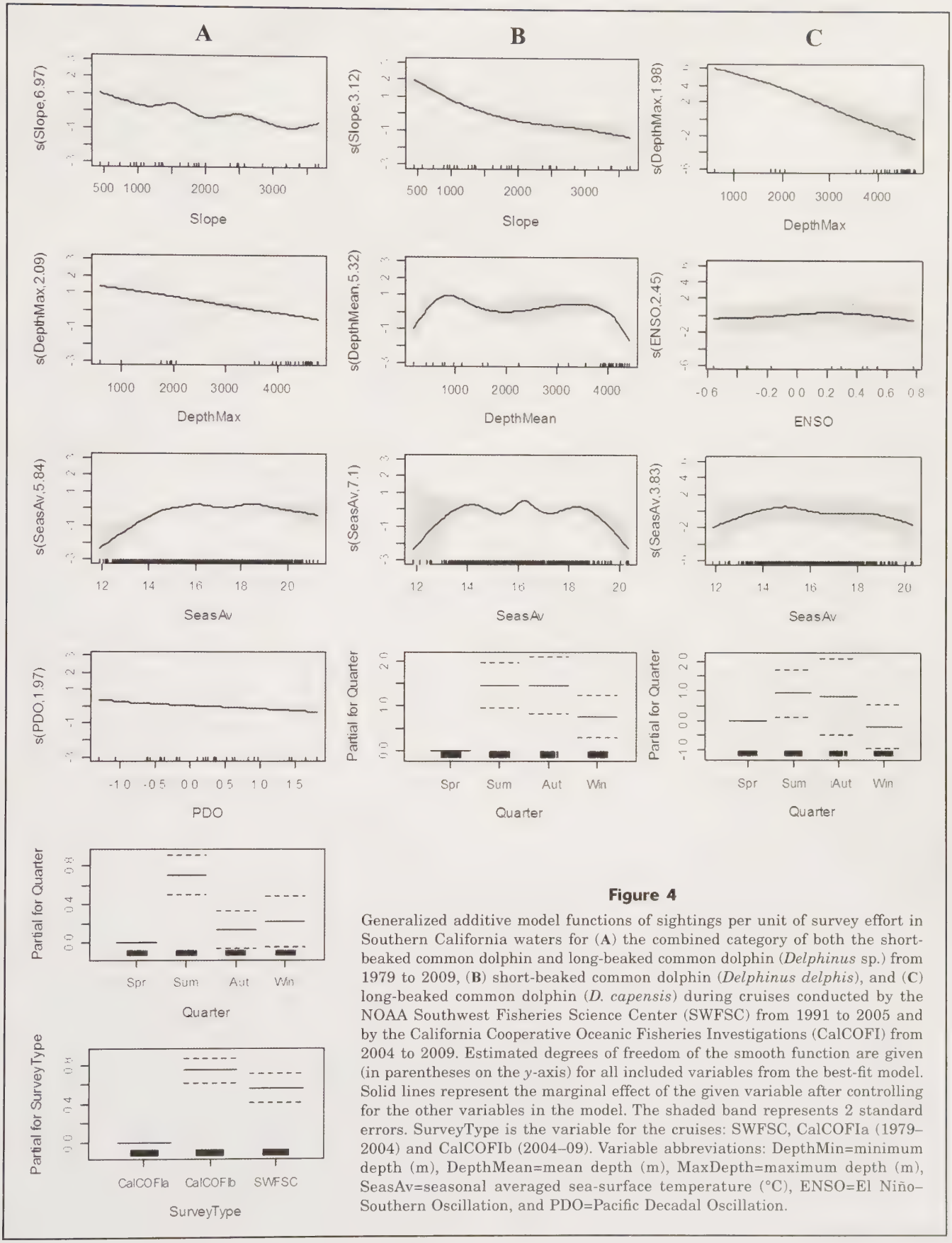

Figure 4

Generalized additive model functions of sightings per unit of survey effort in Southern California waters for (**A**) the combined category of both the short-beaked common dolphin and long-beaked common dolphin (*Delphinus* sp.) from 1979 to 2009, (**B**) short-beaked common dolphin (*Delphinus delphis*), and (**C**) long-beaked common dolphin (*D. capensis*) during cruises conducted by the NOAA Southwest Fisheries Science Center (SWFSC) from 1991 to 2005 and by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) from 2004 to 2009. Estimated degrees of freedom of the smooth function are given (in parentheses on the *y*-axis) for all included variables from the best-fit model. Solid lines represent the marginal effect of the given variable after controlling for the other variables in the model. The shaded band represents 2 standard errors. SurveyType is the variable for the cruises: SWFSC, CalCOFIa (1979–2004) and CalCOFIb (2004–09). Variable abbreviations: DepthMin=minimum depth (m), DepthMean=mean depth (m), MaxDepth=maximum depth (m), SeasAv=seasonal averaged sea-surface temperature (°C), ENSO=El Niño–Southern Oscillation, and PDO=Pacific Decadal Oscillation.

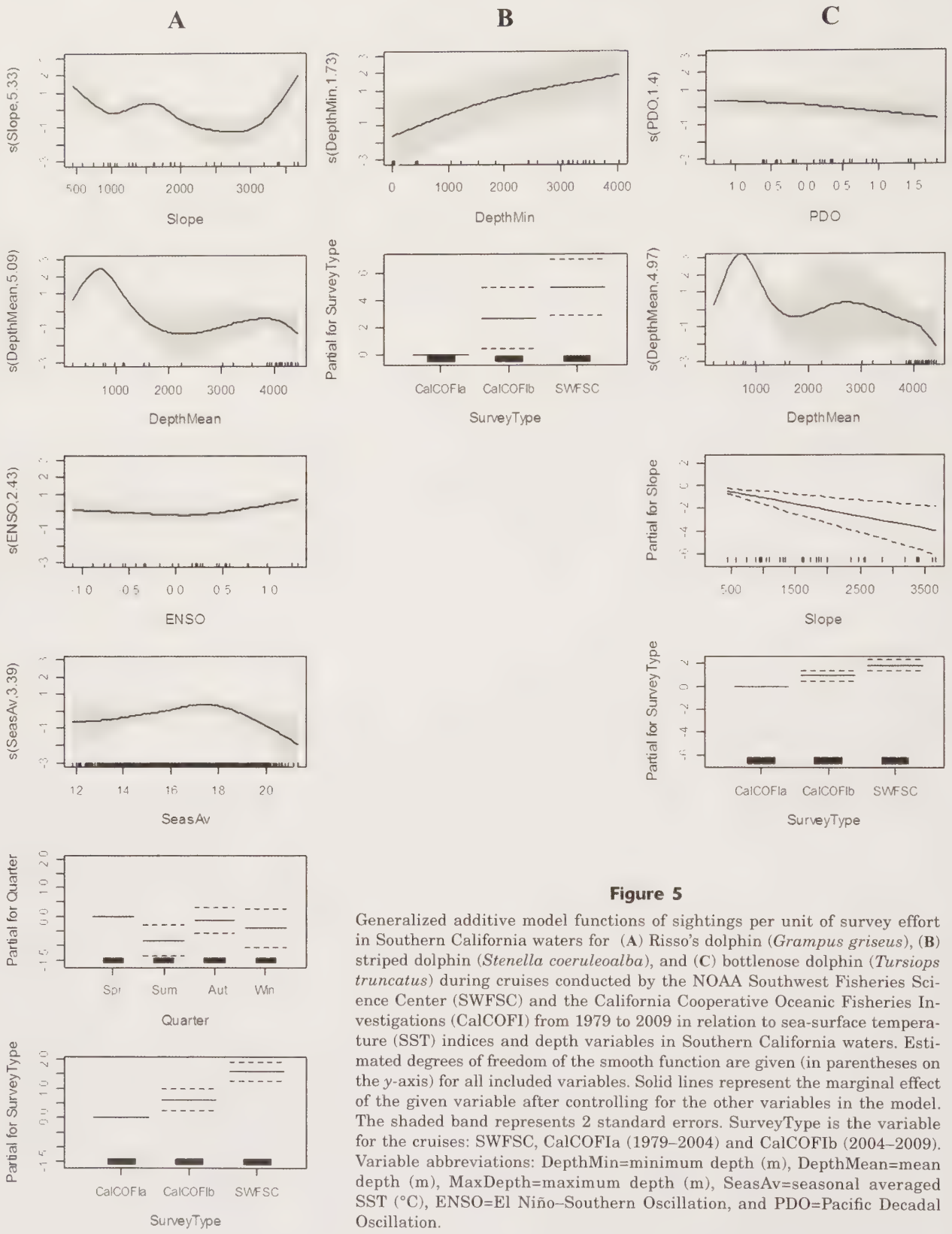

Figure 5

Generalized additive model functions of sightings per unit of survey effort in Southern California waters for (**A**) Risso's dolphin (*Grampus griseus*), (**B**) striped dolphin (*Stenella coeruleoalba*), and (**C**) bottlenose dolphin (*Tursiops truncatus*) during cruises conducted by the NOAA Southwest Fisheries Science Center (SWFSC) and the California Cooperative Oceanic Fisheries Investigations (CalCOFI) from 1979 to 2009 in relation to sea-surface temperature (SST) indices and depth variables in Southern California waters. Estimated degrees of freedom of the smooth function are given (in parentheses on the *y*-axis) for all included variables. Solid lines represent the marginal effect of the given variable after controlling for the other variables in the model. The shaded band represents 2 standard errors. SurveyType is the variable for the cruises: SWFSC, CalCOFIa (1979–2004) and CalCOFIb (2004–2009). Variable abbreviations: DepthMin=minimum depth (m), DepthMean=mean depth (m), MaxDepth=maximum depth (m), SeasAv=seasonal averaged SST (°C), ENSO=El Niño–Southern Oscillation, and PDO=Pacific Decadal Oscillation.

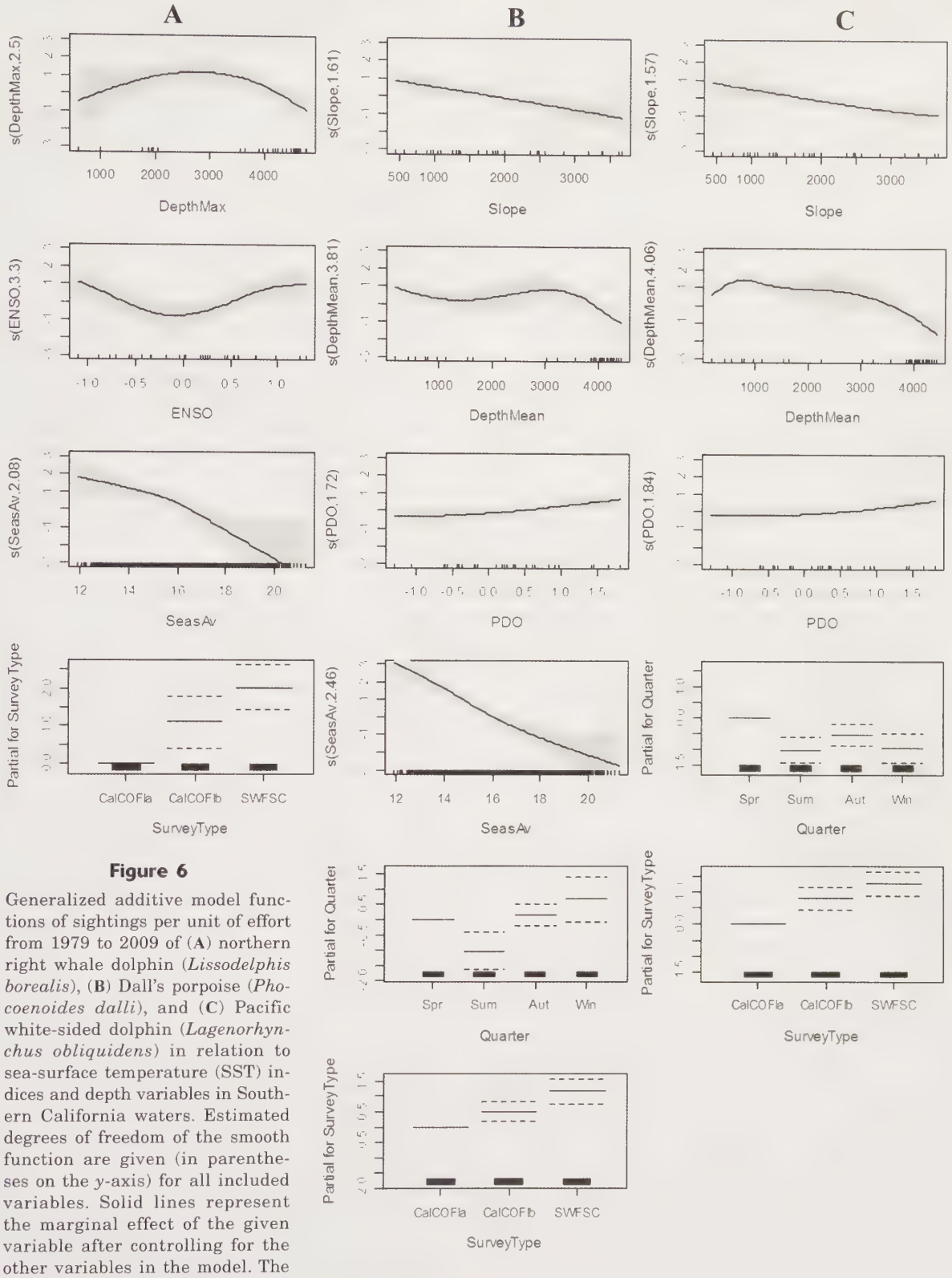

Figure 6

Generalized additive model functions of sightings per unit of effort from 1979 to 2009 of (**A**) northern right whale dolphin (*Lissodelphis borealis*), (**B**) Dall's porpoise (*Phocoenoides dalli*), and (**C**) Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) in relation to sea-surface temperature (SST) indices and depth variables in Southern California waters. Estimated degrees of freedom of the smooth function are given (in parentheses on the *y*-axis) for all included variables. Solid lines represent the marginal effect of the given variable after controlling for the other variables in the model. The shaded band represents 2 standard errors. SurveyType is the variable for the cruises: SWFSC, CalCOFIa (1979–2004) and CalCOFIb (2004–09). Variable abbreviations: DepthMin=minimum depth (m), DepthMean=mean depth (m), MaxDepth=maximum depth (m), SeasAv=seasonal averaged SST (°C), ENSO=El Niño–Southern Oscillation, and PDO=Pacific Decadal Oscillation.

(e.g., Dohl et al., 1986; Barlow, 1995; Forney and Barlow, 1998; Forney, 2000; Barlow and Forney, 2007; Becker, 2007). Risso's and common dolphins preferred waters of intermediate and warmer temperature (14–20°C) (Forney, 2000; Reeves et al., 2002; Becker, 2007). In contrast, sightings of Dall's porpoises, Pacific white-sided dolphins, and northern right whale dolphins peaked in the cool spring season or with cool SSTs. In addition, long-beaked common, bottlenose, and Risso's dolphins and Dall's porpoises showed a preference for inshore or island-associated waters. Short-beaked common and Pacific white-sided dolphins were observed both inshore and slightly offshore. Northern right whale dolphins were associated with the slope region, and striped dolphins were observed only in deep offshore waters. The relationship between SST and depth is complex and difficult to separate, and these models likely oversimplify the observed trends. However, these results do seem to indicate some habitat or resource partitioning is occurring because these small cetacean species presumably follow preferred water conditions and prey.

Although the seasonal distribution patterns here are generally consistent with those found by Forney and Barlow (1998) for temperate species, an increase in common dolphin sightings was observed in that study in winter rather than in summer for 1991–92. In contrast, a summer peak in sightings for common dolphins was found by Dohl et al. (1986). Our results, however, support the findings of both of these studies. ENSO was included as a predictor in the model for the long-beaked common dolphin. The strong El Niño that occurred in 1991–92 may explain the increase in winter sightings for common dolphins in the surveys conducted by Forney and Barlow (1998) over that time period. If the winter of 1991–92 was uncharacteristically warm, then there may have been more common dolphins present than usual at that time of year. In contrast, the 1975–78 surveys conducted by Dohl et al. (1986) overlapped with the 1976–77 PDO regime shift from cool to warm; this shift could account for the increase in common dolphins during the warmer summer months of 1975–78.

Patterns of temperature oscillation

Temperature fluctuation patterns like ENSO, PDO, and the North Atlantic Oscillation have been documented to affect the prey of marine animals. An example of this effect is the strong relationship between the North Atlantic Oscillation, the life cycle of the copepod *Calanus finmarchicus*, and the recruitment of larval Atlantic Cod (*Gadus morhua*) that prey on copepods (Stenseth et al., 2002). Atlantic Cod in turn are a major food source for the gray seal (*Halichoerus grypus*), and *Calanus* spp. are an important prey for the North Atlantic right whale *(Eubalaena glacialis*) (Wishner et al., 1995; Mohn and Bowen, 1996). Calanoid copepods in the California Current system also have exhibited population-level step changes in abundance in response to strong ENSO events and PDO shifts (Rebstock, 2002). For example, during the PDO phase switch in the late 1970s, 28% of the copepod species sampled increased in abundance. In contrast, around 1990 a biological step change occurred in copepod populations, when 28% of the species declined in abundance.

Population fluctuations of small pelagic fishes, such as anchovies (*Engraulis* spp.) and Pacific Sardine (*Sardinops sagax*), are also correlated strongly with both ENSO and PDO indices in the California Current system and in the Peru–Chile Current (Tibby, 1937; Hubbs, 1948; Ñiquen and Bouchon, 2004; Lehodey et al., 2006). These fish species are prey for many species of cetaceans in the California Current, including the short- and long-beaked common dolphins, bottlenose dolphin, Pacific white-sided dolphin, and Dall's porpoise (e.g., Stroud et al., 1981; Walker and Jones, 1993; Heise, 1997; Amano et al., 1998; Osnes-Erie, 1999).

Isolated instances of cetaceans changing their distribution patterns have been noted during and after strong climatic events. One example is the permanent expansion of the northern extent of the range of coastal bottlenose dolphins along the California coast during the 1982–83 El Niño (Defran et al., 1999). Another example is the increased abundance of humpback whales (*Megaptera novaeangliae*) in Monterey Bay during the 1997–98 El Niño (Benson et al., 2002). SST fluctuations have been shown to affect the distribution and community composition of seabirds in the California Current system as well (Hyrenbach and Veit, 2003; Yen et al., 2006). A decline of 2% per year in overall seabird density was recorded for the last 25 years—a drop that was attributed to declines in nearshore abundance of forage fishes (Sydeman et al., in press).

The models for most species included the PDO and ENSO indices as significant variables, although they were not strong predictors in most cases. During positive PDO and ENSO phases, upwelling and productivity decrease while water temperature increases, particularly as warm equatorial waters are pushed poleward and the California Current system is found closer inshore (Sette and Isaacs, 1960; McGowan, 1985). These conditions may explain the apparent association of the Dall's porpoise and Pacific white-sided dolphin with positive PDO indices. These species may be pushed closer to shore by the contraction of the California Current, or they could be concentrating in the remaining areas of productivity, as has been hypothesized for the increase in rorquals in Monterey Bay during the 1997–98 El Niño (Benson et al., 2002).

Alternately, the patterns observed here may reflect changes that occur in other parts of these species' ranges. For example, during negative, cool PDO phases, the overall range of warm-temperate species may contract southward; therefore, a slight increase in the number of common dolphins and even bottlenose dolphins may occur during this phase. Likewise, if the cold-temperate species range as far south as Baja during negative PDO and ENSO periods, then their ranges

may contract northward during positive PDO phases, leading to an increase in sightings of Dall's porpoises and Pacific white-sided dolphins in Southern California waters.

Implications in regard to climate change

We have demonstrated changes in distributions of small cetaceans on scales of months to decades. Despite a limited understanding of the mechanisms behind those changes, the model results may help create a basis for understanding the potential effect of climate change upon these species. Studies of climate change in the California Current system indicate that, in addition to increasing temperatures, a rise in atmospheric carbon dioxide levels is predicted to lead to more intense upwelling (Bakun, 1990; Snyder et al., 2003), stronger thermal stratification, and a deepening of the thermocline (Roemmich and McGowan, 1995). These changes may alter large-scale circulation patterns (Harley et al., 2006). Fluctuations in these physical mechanisms will lead to changes in ecosystem dynamics and biodiversity from primary producers to top predators (Sydeman et al., 2001; Harley et al., 2006; Hooff and Peterson, 2006).

Globally, species associated with sea ice or with highly limited ranges are the most obvious species to be affected by changing ocean temperatures and sea levels (Moore and Huntington, 2008). However, even pelagic species, such as the ones discussed here, are likely to be affected (Learmonth et al., 2006; Simmonds and Eliott, 2009). For example, as water temperatures off Scotland increased, the abundance of common dolphins increased, whereas the number of white-beaked dolphins (*Lagenorhynchus albirostris*), which are associated with cold water, decreased. Such trends could indicate a poleward shift in range for both species (MacLeod et al., 2005; Simmonds and Isaac, 2007). In addition, an influx of cold freshwater in the northern Gulf of Mexico in 2011 may have contributed to an unusually high mortality rate in bottlenose dolphins (Charmichael, et al. 2012).

We predicted that the ranges of the common dolphins, Risso's dolphin, and bottlenose dolphin would expand northward as ocean temperatures warmed, especially as seasonal, ENSO, and PDO events were compounded (e.g., a positive PDO with a positive ENSO). Conversely, we predicted that the ranges of the Pacific white-sided dolphin, northern right whale dolphin, and Dall's porpoise would contract poleward and inshore. These patterns have held true for observations made during previous shorter-term studies. For example, Dall's porpoises and Pacific white-sided dolphins dominated the odontocete species assemblage off central California in the decade before the strong El Niño of 1997–98 (Benson et al., 2002; Keiper et al., 2005).

Keiper et al. (2005) noted that during the strong El Niño of 1997–98 there was a deepened thermocline, a narrow, inshore distribution of Pacific Sardine eggs, and an overall decrease in abundance of macrozooplankton. During that El Niño, sightings of Dall's porpoises were greatly reduced, whereas common and Risso's dolphin sightings increased. Furthermore, Pacific white-sided dolphin sightings decreased after this period, while sightings of common (particularly the long-beaked species) and bottlenose dolphins increased (Keiper et al., 2005).

However, over the longer-term, our study showed an association of the Pacific white-sided dolphin and Dall's porpoise with positive PDO indices, of common and bottlenose dolphins with negative PDO indices, and of the northern right whale dolphin with positive ENSO indices. These results indicate a more complicated relationship between distribution patterns and SST than we allowed for in our initial predictions or that has been observed on shorter temporal scales. Continued monitoring efforts should be made to ensure that future changes in distribution or reproductive success are documented.

Model considerations

The results presented here provide insight into long-term distribution trends of small cetaceans over several decades. The results are both supported by and build upon the current knowledge base for these species. Nonetheless, we recognize some caveats to this study that warrant discussion.

The PDO and ENSO indices were developed with the use of broad regions of the Pacific. Therefore, they may not reflect precisely the specific dynamics of the Southern California study area. The seasonal SSTs, although averaged for each grid section and quarter, were also still quite broad, as was the selected size of grid cells. However, this scope was used intentionally to capture the large temporal- and spatial-scale dynamics of these changing SST patterns, rather than to examine mesoscale dynamics on shorter temporal scales. In addition, the SST, ENSO, and PDO variables have the potential to be correlated, as the indices are similar over time. A correlation analysis was conducted, and correlations between ENSO and PDO and between seasonal SSTs and PDO were detected for some species. In those cases, they were not included together, and only the most significant predictors were included.

Only one cruise occurred per year before 1987. To account for potential differences between Survey Types, we repeatedly reran each model while randomly dropping out data from different years. The results indicated that the models were robust against missing years of data, and the variation in the number of surveys per year did not affect the results. The survey methods from each Survey Type were quite different, making it a challenge to combine these data sets. However, by using only the group SPUE and by limiting our sightings to the ones made in sea states of 3 or less on the Beaufort scale, we tried to make the data as comparable as possible.

The inclusion of the Survey Type variable in most models reflects some of those differences in survey effort. The CalCOFI cruises in 1987–2004 consistently ranked lowest in sighting numbers for all species although those surveys had the most effort. This ranking was likely due to a single observer who covered both birds and mammals with a smaller effective strip width rather than to the multiple observers dedicated to monitoring marine mammals for the other 2 types of surveys.

The SWFSC cruises had the highest number of observations for 6 of the 7 models in which they were included, although those cruises had less effort than the CalCOFI cruises. The high number of observations may have been due to optimal sighting conditions during the SWFSC cruises, which were largely conducted in summer and fall. In addition, big eye binoculars were used on SWFSC cruises but were not used regularly on CalCOFI cruises. In another difference in Survey Type, CalCOFI surveys always were conducted in passing mode in which the survey vessel does not leave the transect line when animals are sighted, but SWFSC ships operated in closing mode and could deviate from the transect line to confirm species.

Finally, we used the number of groups sighted rather than the number of individuals observed as our metric for encounter rate. The correlation analysis did not indicate a strong relationship between the number of groups encountered and the size of the group for any of the modeled species. Therefore, our models may have misidentified trends if a change in group size as a response to any of these variables had better explanatory power than the overall encounter rates.

Conclusions

The models presented in this study indicated that fluctuations in SST regimes influenced the distribution of small cetaceans. However, the relationships were not as straightforward as predicted. The observed complexities likely are related to effects of SSTs on prey and subsequent responses by cetaceans. Dolphins have been shown previously to be sensitive to changes in SST and to shift their distributions in response to regime oscillations like ENSO. However, this study is the first one to model responses to multiple temperature shifts over a long time period for a variety of cetacean species in this region of the California Current system.

The resulting models were unique to each of the 8 species studies. This finding indicates that each species is characterized by a distinct pattern in habitat occurrence related to SST dynamics in this study area, despite the overlap in the overall distributions of the examined species in the Southern California study area. Results herein can be used to begin to predict the future distribution of these small cetaceans throughout the waters off Southern California. Results also provide a tool to understand, as global climate change intensifies, potential responses of these species to rising ocean temperatures and the ecological mechanisms responsible for those responses.

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Appendix I

Search effort (in linear kilometers) and number of groups seen for each species on each of the surveys conducted by the NOAA Southwest Fisheries Science Center (SWFSC) and the California Cooperative Oceanic Fisheries Investigations (CalCOFI) and included in the analyses for this study. El Niño cruises were combined into seasons for analyses. Seasons are defined as follows: spring was February–April, summer was May–July, fall was August–October, and winter was November–January. Species abbreviations are as follows: Dsp=*Delphinus* sp.; Dd=*Delphinus delphis*; Dc=*Delphinus capensis*; Gg=*Grampus griseus;* Lb=*Lissodelphis borealis*; Lo=*Lagenorhynchus obliquidens*; Pd=*Phocoenoides dalli*; Sc=*Stenella coeruleoalba*; Tt=*Tursiops truncatus*. NA=not available. The SWFSC cruises are as follows: CAMMS=The California Marine Mammal Survey; PODS =Population of Delphinus Stocks; ORCAWALE=Oregon, California, Washington Line-Transect and Ecosystem cruise; CSCAPE=The Collaborative Survey of Cetacean Abundance and the Pelagic Ecosystem.

Cruise	Year	Quarter	Dsp	Gg	Lb	Lo	Pd	Sc	Tt	Dd	Dc	Effort (km)
CalCOFI												
CC198705	1987	Spring	5	1	0	0	4	0	3	NA	NA	1559
CC198709	1987	Summer	9	4	0	5	0	0	3	NA	NA	1704
CC198711	1987	Fall	3	1	0	1	2	0	3	NA	NA	1468
CC198801	1988	Winter	3	2	0	2	3	0	3	NA	NA	1501
CC198804	1988	Spring	3	1	4	0	0	0	3	NA	NA	1346
CC198808	1988	Summer	15	0	0	0	3	0	3	NA	NA	1810
CC198810	1988	Fall	3	7	0	0	9	0	3	NA	NA	1420
CC198901	1989	Winter	2	0	1	0	2	0	3	NA	NA	1338
CC198904	1989	Spring	1	0	0	3	7	0	3	NA	NA	1596
CC198907	1989	Summer	25	3	1	1	1	0	3	NA	NA	1932
CC198911	1989	Fall	11	4	1	1	4	0	3	NA	NA	1496
CC199003	1990	Winter	1	0	1	0	1	0	3	NA	NA	407
CC199004	1990	Spring	13	0	0	5	3	1	3	NA	NA	1509
CC199007	1990	Summer	18	2	0	0	1	0	3	NA	NA	1887
CC199011	1990	Fall	5	3	0	1	4	0	3	NA	NA	1349
CC199101	1991	Winter	3	1	0	1	3	0	3	NA	NA	1332
CC199103	1991	Spring	7	2	0	1	5	0	3	NA	NA	1162
CC199107	1991	Summer	28	0	0	2	0	0	3	NA	NA	1668
CC199109	1991	Fall	12	2	0	0	0	0	3	NA	NA	1635
CC199201	1992	Winter	5	1	2	3	1	0	3	NA	NA	1265
CC199204	1992	Spring	5	2	0	1	2	0	3	NA	NA	2427
CC199207	1992	Summer	18	1	1	2	1	0	3	NA	NA	1437
CC199209	1992	Fall	5	0	0	0	2	0	3	NA	NA	1625
CC199301	1993	Winter	10	1	0	1	1	0	3	NA	NA	1249
CC199303	1993	Spring	9	2	0	0	0	0	0	NA	NA	1630
CC199308	1993	Summer	9	0	0	0	0	0	0	NA	NA	1843
CC199310	1993	Fall	2	1	0	0	2	0	0	NA	NA	1549
CC199401	1994	Winter	12	2	2	0	4	0	1	NA	NA	1369
CC199403	1994	Spring	2	0	0	0	0	0	0	NA	NA	1552
CC199410	1994	fall	15	6	0	2	0	0	2	NA	NA	1590
CC199501	1995	Winter	15	2	0	0	1	0	0	NA	NA	1331

Cruise	Year	Quarter	Dsp	Gg	Lb	Lo	Pd	Sc	Tt	Dd	Dc	Effort (km)
CC199504	1995	Spring	12	2	0	0	2	0	0	NA	NA	1629
CC199507	1995	Summer	26	1	0	2	1	0	0	NA	NA	1900
CC199510	1995	Fall	9	1	0	1	0	0	0	NA	NA	1589
CC199604	1996	Spring	6	1	0	0	1	0	1	NA	NA	1214
CC199608	1996	Summer	8	0	0	3	0	0	0	NA	NA	1729
CC199610	1996	Fall	4	0	0	0	0	0	0	NA	NA	1434
CC199701	1997	Winter	7	8	1	5	3	0	0	NA	NA	1442
CC199707	1997	Summer	25	3	0	0	1	0	2	NA	NA	1724
CC199709	1997	Fall	9	1	0	2	0	0	1	NA	NA	1511
CC199712	1997	El Niño 1	2	3	0	0	0	0	0	NA	NA	361
CC199801	1998	Winter	10	1	0	0	0	0	0	NA	NA	696
CC199803	1998	El Niño 2	6	2	0	4	1	0	1	NA	NA	701
CC199804	1998	Spring	13	1	0	2	0	0	1	NA	NA	1491
CC199805	1998	El Niño 3	14	0	0	1	1	0	2	NA	NA	818
CC199806	1998	El Niño 4	14	1	1	2	0	0	1	NA	NA	812
CC199807	1998	Summer	25	0	0	1	0	0	1	NA	NA	1652
CC199809	1998	Fall	9	1	0	0	0	0	0	NA	NA	1499
CC199810	1998	El Niño 5	21	0	0	1	0	0	0	NA	NA	1308
CC199904	1999	Spring	9	1	3	3	1	0	0	NA	NA	1633
CC199908	1999	Summer	33	2	0	0	0	0	1	NA	NA	1457
CC199910	1999	Fall	17	1	0	0	1	0	0	NA	NA	1212
CC200004	2000	Spring	9	0	0	3	5	0	2	NA	NA	1667
CC200007	2000	Summer	9	0	0	10	1	0	3	NA	NA	1754
CC200010	2000	Fall	9	0	2	4	1	0	2	NA	NA	1425
CC200101	2001	Winter	7	2	0	1	1	0	0	NA	NA	1434
CC200104	2001	Spring	5	2	1	1	2	0	0	NA	NA	1428
CC200107	2001	Summer	16	0	0	0	0	0	0	NA	NA	1547
CC200110	2001	Fall	25	3	0	5	0	0	0	NA	NA	1322
CC200201	2002	Winter	7	4	3	0	3	0	1	NA	NA	1172
CC200203	2002	Spring	6	0	0	5	4	0	0	NA	NA	1454
CC200207	2002	Summer	23	1	0	2	2	0	4	NA	NA	1741
CC200211	2002	Fall	7	0	0	0	0	0	0	NA	NA	1443
CC200301	2003	Winter	14	2	0	1	2	0	0	NA	NA	1712
CC200304	2003	Spring	6	3	1	7	12	0	0	NA	NA	3503
CC200307	2003	Summer	16	4	1	0	1	0	0	NA	NA	1680
CC200310	2003	Fall	12	0	0	0	0	0	0	NA	NA	1542
CC200401	2004	Winter	16	1	0	0	4	0	5	NA	NA	1380
CC200403	2004	Spring	13	6	3	7	14	0	0	NA	NA	2301
CC200407	2004	Summer	21	2	0	6	1	2	0	16	0	2003
CC200411	2004	Fall	19	2	0	6	0	0	2	8	8	1552
CC200501	2005	Winter	16	2	1	4	3	0	0	11	1	1376
CC200504	2005	Spring	7	4	6	13	4	0	2	0	4	2024
CC200507	2005	Summer	64	0	0	3	0	0	0	16	18	2264
CC200511	2005	Fall	32	5	1	1	1	0	1	10	7	1357
CC200602	2006	Winter	4	0	0	4	0	0	7	6	4	1292
CC200604	2006	Spring	6	3	2	3	8	0	3	1	1	2070
CC200607	2006	Summer	53	0	0	0	0	0	0	41	3	1964
CC200610	2006	Fall	17	0	1	3	1	1	4	11	2	1731
CC200707	2007	Winter	42	7	0	1	0	0	0	14	10	2180
CC200711	2007	Spring	22	0	2	2	1	0	1	12	0	1630
CC200701	2007	Summer	20	1	0	1	7	0	0	14	0	1454
CC200704	2007	Fall	9	4	1	2	9	0	2	2	1	900
CC200801	2008	Winter	15	4	1	5	4	0	0	8	0	1264
CC200803	2008	Spring	19	2	2	6	22	0	2	13	2	1182
CC200808	2008	Summer	31	1	0	1	0	0	6	10	3	1224
CC200810	2008	Fall	30	2	0	2	0	0	1	21	1	1505
CC200901	2009	Winter	30	1	0	0	13	0	4	18	3	1273
CC200903	2009	Spring	14	0	0	0	2	0	1	5	4	707
CC200907	2009	Summer	34	7	0	0	0	1	7	9	9	931
CC200911	2009	Fall	12	2	1	1	1	0	0	6	1	713
SWFSC 564	1979	Sept–Oct	17	8	1	1	2	1	3	NA	NA	1662

Cruise	Year	Quarter	Dsp	Gg	Lb	Lo	Pd	Sc	Tt	Dd	Dc	Effort (km)
646	1980	June–July	8	0	0	0	2	0	3	NA	NA	2045
798	1982	April	16	15	11	8	16	0	3	NA	NA	1842
674	1983	Dec	19	7	0	18	4	0	3	NA	NA	562
905	1984	Dec	42	13	1	10	3	0	3	NA	NA	1179
CAMMS	1991	July–Oct	50	8	10	0	0	6	3	45	2	4210
PODS	1993	July–Oct	23	3	0	0	0	4	1	21	0	2610
ORCAWALE	1996	Aug–Nov	30	6	1	9	0	6	4	24	2	3936
ORCAWALE	2001	July–Dec	20	7	0	2	0	1	7	16	1	2540
CSCAPE	2005	Aug–Dec	42	2	0	0	6	5	4	29	6	2951

Appendix 2

The effective degrees of freedom (EDF) and *P*-values for each of the parameters included in the generalized additive model of sightings per unit effort in Southern California waters in 1979–2009 for each studied species of small cetacean: short-beaked common dolphin (*Delphinus delphis*), long-beaked common dolphin (*D. capensis*), Risso's dolphin (*Grampus griseus*), striped dolphin (*Stenella coeruleoalba*), bottlenose dolphin (*Tursiops truncatus*), northern right whale dolphin (*Lissodelphis borealis*), Pacific white-sided dolphin (*Lagenorhynchus obliquidens*), and Dall's porpoise (*Phocoenoides dalli*). Because the short- or long-beaked common dolphins were not recognized formally as distinct until 1994, data for both species were used in a combined category in analyses. Note that no EDF was available for the 2 parametric variables (Quarter and SurveyType). SurveyType is the variable for the cruises, which were conducted by the NOAA Southwest Fisheries Science Center and the the California Cooperative Oceanic Fisheries Investigations. Variable abbreviations: DepthMin=minimum depth (m), DepthMean=mean depth (m), MaxDepth=maximum depth (m), SeasAv=seasonal averaged sea-surface temperature (°C), ENSO=El Niño–Southern Oscillation, and PDO=Pacific Decadal Oscillation. NA=not available.

Species	Parameter	EDF	*P*-value
Both common dolphins	Quarter	NA	<0.01
	SurveyType	NA	<0.01
	Slope	6.97	<0.01
	DepthMax	2.09	<0.01
	SeasAv	5.87	<0.01
	PDO	1.97	<0.01
Short-beaked common dolphin	Quarter	NA	<0.01
	Slope	3.12	<0.01
	DepthMean	5.32	<0.01
	SeasAv	7.1	<0.01
Long-beaked common dolphin	Quarter	NA	0.02
	DepthMax	1.98	<0.01
	SeasAv	2.46	0.03
	ENSO	3.82	0.03
Risso's dolphin	Quarter	NA	<0.01
	SurveyType	NA	<0.01
	Slope	5.33	<0.01
	DepthMean	5.09	<0.01
	ENSO	2.43	<0.01
	SeasAv	3.39	0.01
Striped dolphin	SurveyType	NA	<0.01
	DepthMin	1.73	<0.01
Bottlenose dolphin	SurveyType	NA	<0.01
	DepthMean	4.97	<0.01
	PDO	1.4	0.03
Northern right whale dolphin	SurveyType	NA	<0.01
	DepthMax	2.51	<0.01
	ENSO	3.32	<0.01
	SeasAv	2.19	<0.01
Pacific white-sided dolphin	Quarter	NA	<0.01
	SurveyType	NA	<0.01
	Slope	1.57	<0.01
	DepthMean	4.06	<0.01
	PDO	1.84	0.01
Dall's porpoise	Quarter	NA	<0.01
	SurveyType	NA	<0.01
	Slope	1.61	<0.01
	DepthMean	3.81	<0.01
	PDO	1.74	0.01
	SeasAv	2.83	<0.01

Age, growth, and reproduction of Southern Kingfish (*Menticirrhus americanus*): a multivariate comparison with life history patterns in other sciaenids

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Abstract—Southern Kingfish (*Menticirrhus americanus*) is an abundant sciaenid in the northcentral Gulf of Mexico, but little is known of its life history. Our objectives were to describe demographic traits and compare the characteristics of this population with those of other recreationally and commercially important populations in the U.S. Exclusive Economic Zone (U.S. EEZ). We report significant differences in sex-specific weight at length. Otolith annulus formation occurred in April and May and maximum age was 4+ years for both sexes. Length-at-age analysis indicated that mean asymptotic total length (TL; $TL_{\infty, \text{male}}$=244 mm, $TL_{\infty, \text{female}}$=303 mm) and mean instantaneous growth rates (k_{male}=1.12 y^{-1} and k_{female}=0.95 y^{-1}) were significantly different between sexes. The mean length at 50% maturity (TL_{50}) for females was 171 mm TL, corresponding to an age at maturity of 1 year. Gonadosomatic indices and histological examination of ovarian maturity phases indicated rapid gonadal development in February and March with females actively spawning from April to September. The interval between spawning averaged 6.9 days, and the most frequent spawning occurred in June and July. Mean relative batch fecundity was 231.1 number of eggs g^{-1} of ovary-free body weight (±standard error 35.7). Principal component analysis (PCA) of 5 variables from 17 sciaenid populations in the U.S. EEZ identified 2 principal components that explained 68.1% of variation among populations; these components represent a size-related gradient and a gradient of spawning season dynamics. Five distinct groups were identified on the basis of fish size, age at maturity, spawning-season duration, and batch fecundity.

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The family Sciaenidae include many commercially and recreationally important species and occur worldwide in temperate and subtropical marine, estuarine, and fresh waters (Chao, 1995, 2002). There are 79 sciaenids that occur in North America (Page et al., 2013); 36 of these species commonly occur in waters of the U.S. Exclusive Economic Zone (U.S. EEZ), and 29 of those 36 species support either commercial or recreational fisheries or both (FishBase, http://www.fishbase.org). However, only 11 of these fishes are reported individually in the NOAA National Marine Fisheries Service commercial (http://www.st.nmfs.noaa.gov/commercial-fisheries/commercial-landings/annual-landings/index, accessed September 2013) and recreational (http://www.st.nmfs.noaa.gov/st1/recreational/queries/catch, accessed September 2013) statistics databases. Despite the conspicuousness of this family, complete life-history information is not available for many of the commonly occurring species, including some economically important members.

Understanding life-history strategies and the interaction among species traits, environmental factors, and population dynamics is not only important for fisheries management but also vital to predict population responses to a variety of natural and anthropogenic disturbances (Winemiller and Rose, 1992; Winemiller, 2005). A comparison of life-history traits of species within the single, diverse family Sciaenidae can further the understanding of the dynamics of this valuable group of fishes. For example, analysis of the reproductive life-history traits of Sciaenidae in the Gulf of Mexico (GOM) and Caribbean Sea resulted in the recognition of 3 major groups within this family that were defined by maximum length, fecundity, and duration of spawning season (Waggy et al., 2006). Similiarly, Militelli et al. (2013) recently examined reproductive traits of 7 sciaenids from the Buenos Aires, Argentina, coastal zone and found that composite groups could be described on the basis of the length of the reproductive period and size of the spawning area.

Life-history patterns of many of the Sciaenidae in the northcentral GOM are not well understood, and limited life-history information is available on the *Menticirrhus* complex, which includes Gulf Kingfish, (*Menticirrhus littoralis*), Northern Kingfish (*M. saxatilis*), and Southern Kingfish (*M. americanus*). These species are targeted by both recreational and commercial fishermen in Mississippi, and all of them currently are unregulated in the northcentral GOM. Results from analysis of NOAA harvest data for 2000–11 indicate a decline in annual landings of Southern Kingfish from 117,967 to 36,332 kg in Mississippi waters during this time period (http://www.st.nmfs.noaa.gov/st1/recreational/queries/catch, accessed September 2013). This decline likely was affected by a number of factors, and it may be cause for concern for the sustainability of the population.

Southern Kingfish is a widely distributed estuarine sciaenid with a range in coastal waters from southern New England to the southern tip of Florida, the GOM and Caribbean Sea, and as far south as Argentina (Armstrong and Muller[1]; Chao, 2002; Haluch et al., 2011; Militelli et al., 2013); it is the most commonly occurring *Menticirrhus* species in northcentral GOM waters. Although most frequently encountered over sandy bottoms (Chao, 2002), this species has been found in deep channels between barrier islands generally over sand, in shallow muddy bottoms, in seagrasses, or on shell hash (Reid, 1954; Bearden, 1963; Crowe, 1984). Seasonal movements of Southern Kingfish appear to occur from shallow waters, where it occurs in early spring through late fall, to deeper waters during the winter (Hildebrand and Cable, 1934; Bearden, 1963; Lagarde[2]; Fritzsche and Crowe[3]; Crowe, 1984).

Updated information on age, growth, and reproduction of Southern Kingfish in the middle South Atlantic Bight (SAB) was published last year (McDowell and Robillard, 2013) and includes the first age estimates from otoliths and fecundity estimates. However, similar current information, including histological assessment, for Southern Kingfish in the GOM had not been completed until we concluded the study presented here. McDowell and Robillard (2013) reported that the spawning season for this species in the SAB was March–August and that peak activity occurred in April. That finding is similar to previous results from studies in the GOM; for those studies gonads were examined macroscopically and indicated that the spawning season in the GOM lasts from February or March to November (Irwin, 1970; Crowe, 1984; Harding and Chittenden, 1987), with a peak in April (Fritzsche and Crowe[3]). Size at sexual maturity appears similar between the GOM and the SAB; Harding and Chittenden (1987) reported on the basis of macroscopic assessment that females in the northwestern GOM reach 100% maturity at an age of 12–14 months or a size of 250 mm total length (TL), and McDowell and Robillard (2013) suggested that females from the SAB reach 50% maturity at 1.1 years or 199 mm TL.

Knowledge of the reproductive biology and somatic traits of fish populations is required to assess the resiliency of populations to fishing (Nielsen and Johnson, 1983; Fulford and Hendon, 2010). To address gaps in knowledge, we describe a variety of reproductive and somatic traits, namely annual spawning season, spawning frequency, batch fecundity, and size at 50% maturity, for Southern Kingfish within the northcentral GOM that were determined by histological analysis and with standard techniques. We also quantified length at age and weight at length from analyses of nonlinear relationships. Finally, we compare these traits with traits of other recreationally and commercially important sciaenid populations in the U.S. EEZ to assess differences and similarities in life-history patterns of members of this family.

Materials and methods

Southern Kingfish were sampled from several locations in the Mississippi Sound off the coast of Mississippi from April 2008 to May 2009 (Fig. 1). We targeted with hook and line a minimum of 50 fish each month from February to October and 15 fish from November to January. Haphazardly collected samples from crab pots and otter trawls during spring and summer were also obtained. Fish were identified according to Chao (2002). Upon collection, fish were immediately placed on ice and processed in the laboratory within 24 h. Each fish was measured for TL and standard length (SL) in millimeters and weighed in grams. The left sagittal otoliths of these fish were removed, cleaned, and dried; sex was determined macroscopically when gonads were removed and weighed (0.1 g). Sex-specific gonadosomatic indices (GSIs) were calculated:

$$GSI = (GW/GFBW) \times 100, \quad (1)$$

where GW = gonad weight; and
$GFBW$ = gonad-free body weight of the fish (Greeley et al., 1986).

A small cross section from the middle of the right gonad was removed and fixed in 10% neutral buffered

[1] Armstrong, M. P., and R. G. Muller. 1996. A summary of biological information for southern kingfish (*Menticirrhus americanus*), Gulf kingfish (*M. littoralis*), and northern kingfish (*M. saxatilis*) in Florida waters. Florida Marine Research Institute (FMRI) In-house Report IHR 1996-004, 25 p. [Available from http://research.myfwc.com/publications/publication_info.asp?id=43619.]

[2] Lagarde, C. C. 1981. Environmental requirements of selected coastal finfish and shellfish of the Mississippi Sound and vicinity: Southern kingfish *Menticirrhus americanus* (Linnaeus), 5 p. [Available from Mississippi State Univ. Research Center, NSTL Station, Mississippi, 105 Mill St.; Starkville, MS 39759.]

[3] Fritzsche, R. A., and B. J. Crowe. 1981. Contributions of the life history of the southern kingfish, *Menticirrhus americanus* (Linnaeus), in Mississippi, 84 p. BMR Project No. CO-ST-79-022. [Available from Mississippi Department of Marine Resources, 1141 Bayview Ave.; Biloxi, MS 39532.]

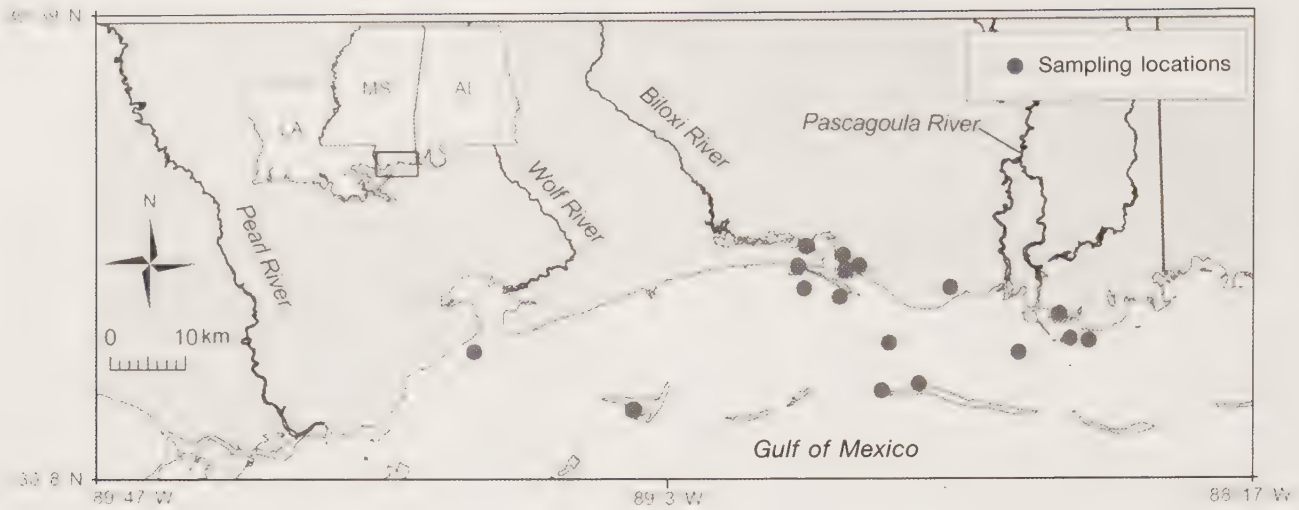


Figure 1

Map of locations where Southern Kingfish (*Menticirrhus americanus*) were sampled with hook and line and crab pots between April 2008 and May 2009 in the Mississippi Sound, Mississippi, to describe reproductive and somatic traits of this species and compare its life history with that of other sciaenids.

formalin for a minimum of 1 week for histological analysis.

Aging and aging validation of otoliths

Age estimates were determined from Southern Kingfish allocated in 10-mm-TL size classes. We randomly chose and aged up to 5 specimens per size bin; otoliths were processed as described in VanderKooy (2009). Otoliths were embedded in a resin block (Buehler Epoxicure[4] resin and hardener, Buehler, an ITW Co., Lake Bluff, IL) and sectioned at the junction of the ostium and sulcus with a saw equipped with a Norton diamond wheel (Saint-Gobain, Valley Forge, PA). These sections were sanded, mounted on labeled slides with clear Crystalbond 509 adhesive (Aremco Products, Inc., Valley Cottage, NY), and the slide was cooled and dried. The otolith sections were polished with a clear Flox-Texx mounting medium (Thermo Fisher Scientific, Inc., Waltham, MA).

Annuli were counted with a Motic BA200 microscope (Motic North America, Richmond, Canada) under transmitted light by 2 independent readers. Fully formed annuli were counted to determine the age of the fish specimen, and the outer edge margin was coded on the basis of the percentage of translucent area beyond the final opaque ring (margin codes: 1=0%, 2=33%, 3=66%, and 4=99%; [VanderKooy, 2009]). A margin code of 1 was assumed to signify the month the annulus was formed. Numbers of annuli and margin codes were compared between readers, and any discrepancies were reexamined by a third reader; if agreement could not be reached, the otolith was removed from analysis. McDowell and Robillard (2013) validated that Southern Kingfish off Georgia produced a single annulus once a year.

Reproductive biology

Preserved ovaries were dehydrated, embedded in paraffin, sectioned at 4 μm, and stained with Hematoxylin 2 and Eosin Y (Thermo Fisher Scientific) for histological examination. Slides were assessed microscopically to determine ovarian phases defined by Brown-Peterson et al. (2011); the 5 reproductive phases of immature, developing, spawning capable, regressing, and regenerating, as well as the associated subphases of early developing and actively spawning, were recognized. A Southern Kingfish was defined as sexually mature once it entered the developing phase (DE) and cortical alveoli (CA) oocytes were observed.

Two quantitative approaches were used to estimate the spawning frequency of Southern Kingfish: 1) the percentage of fish in the spawning-capable phase with or without a 24-h postovulatory follicle (POF) complex (hereafter termed the POF method) and 2) the percentage of fish undergoing oocyte maturation (OM) (Hunter and Macewicz, 1985) (hereafter termed the OM method). Spawning frequency is expressed as the number of days between spawning events (see Brown-Peterson and Warren [2001] for details).

Batch fecundity (BF) was estimated for female Southern Kingfish in the actively spawning subphase. A subsample from the middle of the gonad was removed, weighed (to the nearest 0.1 g), and preserved

[4] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

in modified Gilson's fluid (Bagenal, 1966) for a minimum of 3 months. Once oocytes were separated from ovarian tissue, they were suspended in water and all hydrated or OM oocytes occurring in six 1-mL aliquots were counted. Graphs of oocyte size-frequency distributions of spawning-capable and actively spawning fish were developed to identify and determine the size of OM oocytes used for counts. Batch fecundity (number of eggs) and relative batch fecundity (RBF; number of eggs per gram of ovary-free body weight [eggs g^{-1} OFBW]) were calculated by the volumetric method (Bagenal and Braum, 1971). All values for BF and RBF provided here are reported as a mean ± standard error of the mean (SE).

Comparison of sciaenid life histories

Life-history data were summarized for recreationally and commercially important sciaenid species commonly occurring in the U.S. EEZ. Species that occur infrequently in U.S. catches, have their centers of distribution outside U.S. waters, or that are important only in the aquarium trade, were excluded from the comparison. In addition, commercially or recreationally important species for which there is little life-history information were excluded from the data summary. To treat geographically separated populations of the same species individually, we recognized GOM, Pacific, and Atlantic populations within species. Data for each of these species were obtained from the literature, with the exception of Southern Kingfish, which is described in this study. We summarized 8 somatic and reproductive traits for each species: 1) maximum age (years), 2) maximum TL (millimeters), 3) spawning-season duration (months), 4) spawning frequency (days), 5) RBF (eggs g^{-1} OFBW), 6) age at maturity (years), 7) TL at maturity (millimeters), and 8) the parameter b (morphology index: exponent of weight at length from the power function) in the 2-parameter power function used to describe weight at length ($W=aTL^b$).

Data analyses

Somatic patterns of Southern Kingfish were quantified with linear and nonlinear relationships. The mean TL at 50% maturity (TL_{50}) was estimated with a 2-parameter logistic model:

$$M_{TL} = \frac{1}{1+e^{-r(TL-TL_{50})}}, \quad (2)$$

where female maturity was coded binomially as immature (0) or mature (1).

The relationship between sex-specific SL and TL was estimated with a linear model:

$$SL = \beta_0 + \beta_1 \times TL. \quad (3)$$

We used a 2-parameter von Bertalanffy growth function (VBGF) to describe length at age:

$$TL_t = TL_\infty(1-e^{-kt}), \quad (4)$$

where TL_t = TL of a fish with age t:

The VBGF model parameters were TL_∞ (the mean hypothetical maximum TL achieved by an individual, in millimeters) and the growth coefficient k (the rate of growth, per year). We estimated longevity as the age (in years) taken to reach 95% and 99% of predicted TL_∞ (Fabens, 1965; Ricker, 1979) and used a power function to determine mean weight at length. The 95% confidence intervals (CI) of the mean model parameters for the VBGF, power, and logistic functions were determined by using the confint algorithm distributed in the stats package in the base version of the program R (vers. 2.15.1; R Core Team, 2012).

The GSI values were arcsine square-root transformed before analysis and were tested for normality (Kolmogorov-Smirnov one-sample test) and homogeneity of variance (Levene's test). A one-way analysis of variance (ANOVA) tested for GSI differences among months by sex. If a significant F-value was observed, monthly values were separated with a Sidak pairwise test; if the data were heterogeneous, a Games-Howell (GH) test was used (Field, 2005). Differences in spawning frequency among seasons (early, mid, and late) were tested with a chi-square test. Linear regressions of $\log_{10}$-transformed data were used to determine if there were relationships between either BF or RBF as the dependent variable and TL, OFBW, and age as the independent variables. The SPSS program (vers. 20.0; IBM Corp., Armonk, NY) was used, and the significance level was $P<0.05$.

Principal components analysis (PCA) was used to compare and describe the multivariate somatic and reproductive traits of 17 geographic populations (14 species) in the family Sciaenidae. We limited our PCA to those populations that had available data for 5 somatic and reproductive traits. Somatic traits included the maximum TL and the parameter b; reproductive traits included duration of spawning season, RBF, and age at maturity. In cases where more than one value was reported for a trait, the median value was used for the PCA. The PCA was performed by eigenvalue decomposition of the correlation matrix with varimax rotation to maximally resolve loadings, and only eigenvalues >1.0 were used. We considered any variable that loaded on a component at $|\geq 0.60|$ to make a significant contribution to interpretation of that component (Hair et al., 1984). The SPSS program was used, and the significance level was $P<0.05$.

Results

Somatic characteristics

From April 2008 to May 2009, 519 Southern Kingfish (434 females, 85 males) were sampled; no fish were collected in January 2009. Of these fish, 508 were collect-

Table 1

Sample size (n), mean total length (TL, in millimeters) and minimum and maximum TL values by month and sex for Southern Kingfish (*Menticirrhus americanus*) collected in Mississippi Sound, Mississippi, from April 2008 to May 2009.

	Female				Male			
Date	n	Mean TL	Min TL	Max TL	n	Mean TL	Min TL	Max TL
April 2008	45	232	192	267	3	234	227	244
May 2008	3	270	231	303	–	–	–	–
June 2008	45	217	164	312	29	193	173	224
July 2008	42	243	163	348	10	226	180	256
August 2008	33	254	219	331	7	231	212	267
September 2008	51	252	191	328	3	233	226	242
October 2008	49	238	182	341	6	222	215	240
November 2008	16	258	205	307	2	212	203	220
December 2008	3	266	246	278	2	233	221	244
February 2009	45	239	181	283	10	217	198	263
March 2009	49	229	135	279	6	210	171	244
April 2009	11	246	148	280	2	199	198	200
May 2009	42	232	184	300	5	207	191	224
Overall	434	–	135	348	85	–	171	267

ed with hook and line, 7 were collected in otter trawls, and 4 were collected from crab pots. All haphazardly sampled specimens were within the normal size distribution (trawls, 187–300 mm TL; crab pots, 263–280 mm TL). Sizes of females were recorded in ranges of 135–348 mm TL and 24.8–530.2 g; males fell in size ranges of 171–267 mm TL and 49.4–213.4 g (Table 1; Fig. 2, A and B). There was a significant linear relationship between TL and SL for both sexes (Table 2; males: $P<0.0001$, coefficient of multiple determination [R^2]=0.98; females: $P<0.0001$, $R^2=0.96$).

Comparison of the mean values and confidence intervals derived in the VBGF analysis indicated that males reach a significantly smaller asymptotic TL ($\alpha=0.05$) and grow faster than females (Fig. 2, A and B; Table 2). Females at all ages had a greater mean length than that of males (Fig. 2C). The estimated longevity, calculated with the mean VBGF parameters, was 3.1–4.3 years for males and 3.6–5.1 years for females (Table 2). Significant differences in both a and b parameters were observed by comparing mean and 95% CI values in the weight-at-length relationship (parameter a was the coefficient of the power function). Females had a significantly greater mean value of the power function exponent (parameter b) than had males: 3.26 versus 2.88 ($\alpha=0.05$; Table 2).

Age determined from otoliths

Alternating opaque and translucent annuli were distinctive in the prepared cross sections of Southern Kingfish otoliths (Fig. 3A). Marginal increment analysis showed that Southern Kingfish in the GOM form opaque annuli during April and May, on the basis of the presence of fish with a margin code of 1 (0% translucence above the opaque annulus; Fig. 3B). A single fish had a margin code of 1 in June, although 2 was the dominant margin code in June and July (78% and 73% of fish, respectively). Fish with a margin code of 2 showed active accretion of the otolith beyond the formation of the opaque annulus. Margin codes 3 and 4 were most common from August to March; margin code 4 was dominant in February and March, just before the deposition of the opaque annulus (Fig. 3B).

There were 5 age classes (age 0–4) observed in the sampled mature population ($n=123$) of Southern Kingfish in the northcentral GOM. Fish of age 1 and 2 were the largest groups, accounting for 39% and 33% of the total, respectively. Because of the sampling technique used, young-of-the-year (age-0) fish composed only 12%, and fish of age 3 and 4 represented 13% and 3% of the sample, respectively.

Reproductive characteristics

Of the 519 Southern Kingfish collected, ovary samples from 397 females were processed for histological analysis. The smallest female observed to reach sexual maturity was 163 mm TL and age 1. Only 3.5% of the 397 females histologically examined were found to be immature. Estimated size at L_{50} was 171 mm TL (Fig. 4; $R^2=0.71$, $n=396$). All females >211 mm TL were sexually mature and were age 1 or older.

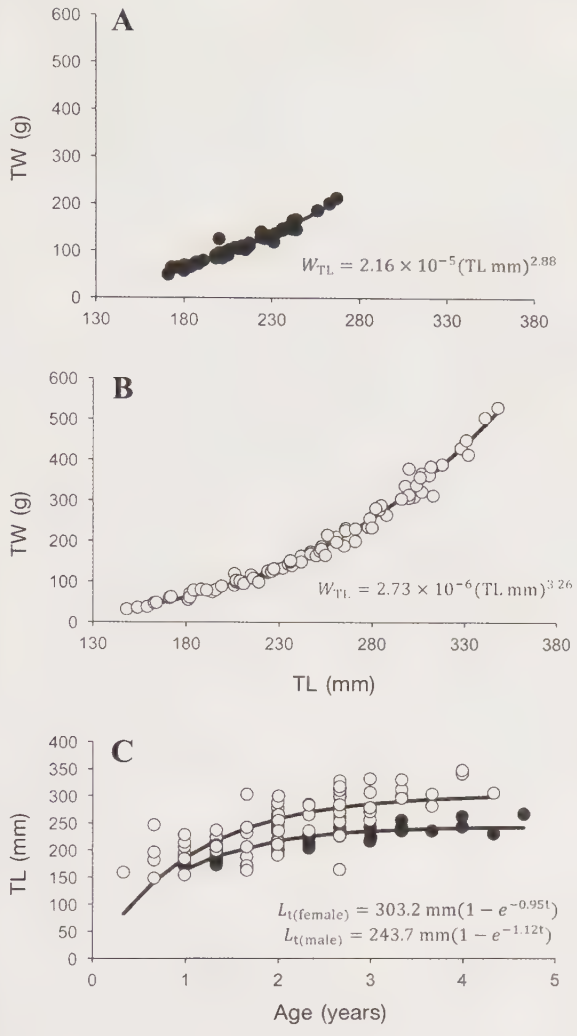


Figure 2

Somatic relationships for Southern Kingfish (*Menticirrhus americanus*) collected in the Mississippi Sound, Mississippi, between April 2008 and May 2009: (**A**) weight-at-length relationships for males (total weight [TW] versus total length [TL]), (**B**) weight-at-length relationships for females, and (**C**) age in relation to TL for males (n=43, dark circles) and females (n=80, open circles).

Female GSI increased from February to April, remained relatively high from May to August, and decreased thereafter (Fig. 5A). Female GSI among months was significantly different (ANOVA: $F_{10,\ 423}$=32.49; P<0.0001) with values for March–September significantly higher than those for all other months (GH, P<0.05), indicating Southern Kingfish may spawn in the northcentral GOM from March to September. Male GSI mirrored that of females (Fig. 5A) and was significantly different among months (ANOVA: $F_{10,\ 74}$=7.65; P<0.0001), peaking in April and reaching the lowest values in November (Sidak; P<0.05).

Histological analysis confirmed the Southern Kingfish spawning season that had been indicated by GSI value in our analysis. The majority of the females were in the early developing subphase in February; this percentage decreased in March as fish moved into the developing phase (Table 3). Females were first observed in the spawning capable phase (Fig. 5B) in March, although no POFs were seen in March. From April to August, ≥78% of captured females were in the spawning-capable phase; this percentage decreased to 59% by September (Table 3). Females in the actively spawning subphase were found from April to September (Table 3). Although some females were found in the spawning-capable phase in October (13%), the majority of fish were in the regressing and regenerating phases, signaling the end of the reproductive season. By November, all females were reproductively inactive (Table 3). Therefore, on the basis of histological observations, the spawning season for Southern Kingfish in the northcentral GOM appears to be April–September. Furthermore, the asynchronous oocyte development observed in females in the spawning-capable phase (Figs. 5B and 6) indicates that Southern Kingfish is a batch-spawning species in the northcentral GOM.

Seasonal spawning frequencies were estimated with both the POF and OM calculation methods, and they were calculated only for months when actively spawning females were observed (Table 4). Results were similar between methods for the early and mid-season spawning frequencies but differed during the late season. There was a significant difference seasonally for frequencies calculated with the POF method (χ^2=17.50, df=2, P<0.0001) but not for values estimated with the OM method (χ^2=3.251, df=2, P>0.05). Both methods revealed a spawning frequency of 11.3 days between spawns for the early season (April–May). During the mid-season (June–July), spawning frequency ranged from 3.5 to 5.8 days between spawnings depending on the method. Spawning frequency in the late season (August–September) was much greater for the OM method (5.4 days) compared with the POF method (19.7 days). The mean annual spawning frequency was calculated for both methods at 6.9 days between spawnings (Table 4). Therefore, over the course of the entire spawning season (April–September), Southern Kingfish spawn on average once every 7 days and an individual has the potential to spawn 26 times.

Batch fecundity estimates were compared for 11 females that were in the actively spawning subphase. A distinct group of oocytes >350 µm was observed in actively spawning fish; therefore, oocytes >350 µm were considered to be undergoing OM (Fig. 6) and were counted for fecundity analysis. Overall BF ranged from 17,338 to 80,495 eggs and had a mean of 35,571 eggs (SE 6405) (Table 5). There were no significant relationships between $\log_{10}$ BF and $\log_{10}$ TL (R^2=0.199, $F_{1,9}$=2.23, P=0.169) or $\log_{10}$ BF and $\log_{10}$ OFBW

Table 2

Summary of equations and related statistics used in this study for analyses of Southern Kingfish (*Menticirrhus americanus*) collected in Mississippi Sound, Mississippi, between April 2008 and May 2009. W=somatic wet weight (in grams), TL=total length (in millimeters), SL=standard length (in millimeters), coefficient of multiple determination (R^2), coefficient of correlation (r), CI=confidence intervals, y=year, β_1=slope of simple linear regression, β_0=y-intercept of simple linear regression, k=is a growth rate constant (y^{-1}), TL_∞=is the mean maximum TL (mm), TL_t=TL at time t (mm), t=time, r=instantaneous rate of increase (mm^{-1}), a= coefficient of the power function, b= exponent of the power function, TL_{50}= total length at 50% maturity, $\rho_{95\%}$ and $\rho_{99\%}$= the age (y) taken to reach 95% and 99% of predicted TL_∞.

Analysis	Model name (model formulation)	Sex	n	R^2	P	Parameter	Estimated mean parameter value (minimum to maximum 95% CI)
SL vs. TL	Linear $SL = \beta_0 + \beta_1 \times TL$	Female	434	0.96	<0.001	β_0	−6.26 (−10.43 to −2.08)
						β_1	0.85 (0.83 to 0.87)
		Male	85	0.98	<0.001	β_0	−8.26 (−13.45 to −3.08)
						β_1	0.86 (0.84 to 0.89)
Length-at-age	2-parameter von Bertalanffy growth function $TL_t = TL_\infty(1 - e^{-kt})$	Female	89	0.57	–	k	0.95 y^{-1} (0.76 to 1.16 y^{-1})
						TL_∞	303.2 mm (284.7 to 328.6 mm)
		Male	43	0.75	–	k	1.12 y^{-1} (0.99 to 1.26 y^{-1})
						TL_∞	243.7 mm (235.6 to 252.7 mm)
Weight at length	Power function $W = aTL^b$	Female	80	0.98	–	a	2.73×10^{-6} (1.42×10^{-6} to 4.78×10^{-6})
						b	3.26 (3.16 to 3.37)
		Male	43	0.96	–	a	2.16×10^{-5} (7.14×10^{-6} to 5.48×10^{-5})
						b	2.88 (2.71 to 3.09)
Longevity	95% and 99% of predicted L_∞	Female	–	–	–	$\beta_{95\%}$	3.6 y
						$\beta_{99\%}$	5.1 y
		Male	–	–	–	$\beta_{95\%}$	3.1 y
						$\beta_{99\%}$	4.3 y
Maturity	2-parameter logistic function $M_{TL} = (1 + e^{-r(TL - TL_{50})})^{-1}$	Female	396	0.37	–	r	0.71 y^{-1} (0.06 to 0.09 y^{-1})
						TL_{50}	170.6 mm (166.8 to 176.6 mm)

Table 3

Percentages of spawning female Southern Kingfish (*Menticirrhus americanus*) by month and spawning phase on the basis of histological analysis. Samples were collected in Mississippi Sound, Mississippi, between April 2008 and May 2009. Actively spawning is a subphase of the spawning-capable phase.

Spawning phases	Month	Feb.	Mar.	Apr.	May	Jun.	July	Aug.	Sep.	Oct.	Nov.	Dec.
	n	44	49	44	45	40	41	33	49	37	13	2
Immature		2	6	2	13	2	5	0	0	0	0	0
Developing		2	31	0	0	2	0	0	0	3	0	0
Early developing		64	24	5	2	8	0	0	0	0	0	0
Spawning-capable		0	39	86	76	63	80	76	47	13	0	0
Actively spawning		0	0	7	9	15	15	15	12	0	0	0
Regressing		0	0	0	0	10	0	0	8	35	8	0
Regenerating		32	0	0	0	0	0	9	33	49	92	100

Figure 3

Image of a sagittal otolith and a plot of marginal increments (shown by code) from Southern Kingfish (*Menticirrhus americanus*) collected in Mississippi Sound, Mississippi, between April 2008 and May 2009. (**A**) Transverse section of a sagittal otolith on a Southern Kingfish that was 4+ years old, with the numbered arrows indicating deposited annuli and MC 3 indicating the margin code. (**B**) Percentage of fish in each marginal increment group, pooled by gender and age, from February to November. There were no data for December and January. Margin codes are based on the percentage of translucent area beyond the final opaque ring of the otolith (margin code 1=0%, 2=33%, 3=66%, and 4=99%). The numbers above the bars represent, for each month, the number of otoliths analyzed for marginal increments.

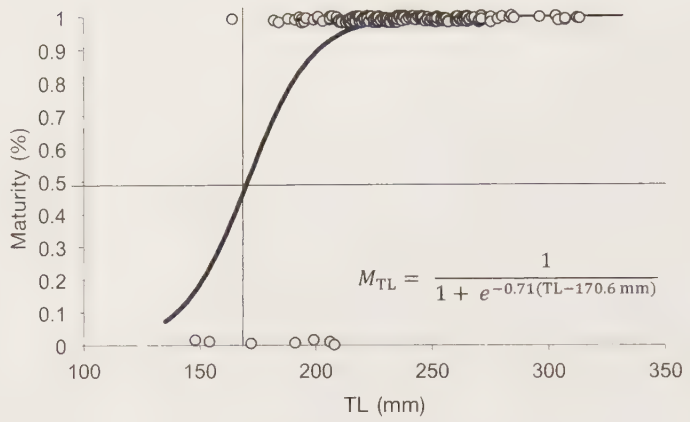


Figure 4

Plot of percentage of female Southern Kingfish (*Menticirrhus americanus*) collected from the Mississippi Sound, Mississippi, between April 2008 and May 2009 that reached maturity (entered the reproductive cycle) in relation to total length (TL) by 10-mm-TL size bins. The vertical line at 171 mm TL indicates the TL where 50% of individuals were mature (TL_{50}).

(R^2=0.164, $F_{1,\ 9}$=1.77, P=0.216). The 11 specimens used in the fecundity calculations were collected in May, July, August, and September, and the highest mean BF occurred in August at 38,722 eggs (SE 20,288) and the lowest mean BF, in September at 33,730 eggs (SE 12,544). There were only 2 age classes represented in the fecundity analysis: age-1 (n=4) and age-2 (n=7) fish (Table 5). Mean BF was slightly higher in age-2 fish at 36,622 eggs (SE 6122) than in age-1 fish at 33,730 eggs (SE 15,591); however, there was no significant relationship between $\log_{10}$ BF and $\log_{10}$ age (R^2=0.015, $F_{1,\ 9}$=0.136, P=0.721).

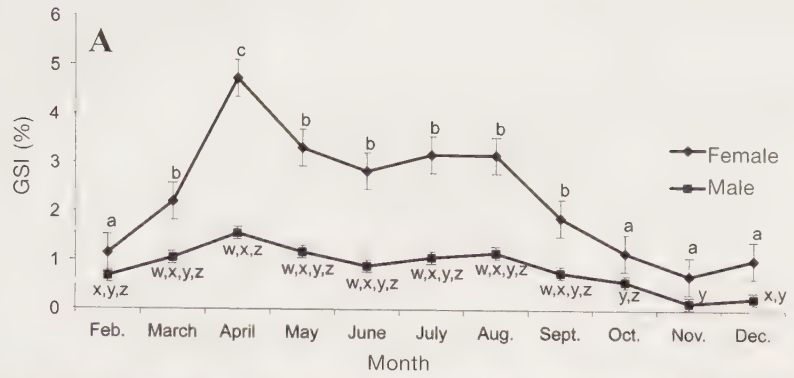
Relative batch fecundity had a range of 94.4–509.5 eggs g^{-1} OFBW and a mean of 213.1 eggs g^{-1} OFBW (SE 35.7) (Table 5). Like the BF results, results for RBF had its highest mean in August at 259.6 eggs g^{-1} OFBW (SE 124.9) and lowest mean in September at 168.1 eggs g^{-1} OFBW (SE 70.3). Unlike the BF results, results for mean RBF were lower in age-2 fish, with 200.2 eggs g^{-1} OFBW (SE 29.4), than in age-1 fish, with 235.7 eggs g^{-1} OFBW (SE 91.5). Potential annual fecundity for Southern Kingfish in the northcentral GOM indicates that a female with a somatic wet weight of 176 g could potentially spawn 924,846 eggs over the course of the spawning season.

Sciaenidae life-history traits: a comparative analysis

Wide variation was observed in the somatic and reproductive traits examined for the 21 sciaenid populations that were analyzed in this study (Appendix table). For instance, Silver Seatrout (*Cynoscion nothus*), a GOM species, has the lowest reported maximum age (1.5 years) of the 21 species, but Black Drum (*Pogonias cromis*), another GOM species, has the oldest reported maximum age (43 years). Duration of spawning season ranged from 2 months (Black Drum) to 7–10 months for White Croaker (*Genyonemus lineatus*), a Pacific species. Size at maturity varied from 110–120 mm TL in Silver Perch (*Bairdiella chrysoura*), a GOM species, to 900 mm TL for Atlantic populations of the Red Drum (*Sciaenops ocellatus*). Life-history traits least frequently reported for sciaenid species include RBF and spawning frequency (Appendix table). Of the 11 species or populations with available spawning-frequency data, Queenfish (*Seriphus politus*) has the longest interspawning interval of 7.4 days and Silver Perch has the shortest interval of 1.3–1.6 days.

The PCA of the 5 somatic and reproductive traits produced 2 meaningful components that accounted for 68.1% of the total variation of the original data set. The first principal component (PC 1) accounted for 43.1%, whereas the second principal component (PC 2) accounted for 25.0%. Maximum TL and age at maturity both positively loaded on PC 1, but RBF loaded negatively on PC 1 (Table 6). In contrast, duration of spawning season and parameter b loaded positively on PC 2 (Table 6). We interpret PC 1 as a size-related component of life history, and PC 2 represents spawning season dynamics. Overall, the PCA indicated 3 general trends in sciaenid life history: 1) fishes that reach a larger maximum TL and older age at maturity tend to have lower RBF, 2) a higher RBF is associated with a shorter spawning-season duration, and 3) a longer spawning-season duration is associated with fishes that have higher b values.

Five groups of sciaenid populations can be discerned in the PCA biplot (Fig. 7). Group A, consisting of fishes with high maximum TL, greater age at maturity, and low RBF, is composed of GOM species Red Drum and Black Drum. Group B consists of fishes with longer spawning seasons, greater b values, low RBF, smaller maximum TL, and lower age at maturity and is represented by Sand Seatrout (*Cynoscion arenarius*), Southern Kingfish, White Croaker, and Queenfish, a mixture of species from all 3 regions, the GOM as well as the Atlantic and Pacific. Group C, made up of fishes with higher RBF, shorter spawning season, young age at maturity, small maximum TL, and low b values, is represented by 2 GOM species: Spot (*Leiostomus xanthurus*) and Silver Perch. Group D consists of fishes with more intermediate traits, such as small maximum TL, low age at maturity, and moderate spawning season, b values, and RBF. A species each from the Atlantic and GOM represent group D: Atlantic Croaker (*Micropogonias undulatus*) and Silver Seatrout. Finally, group E also is an intermediate group with characteristics of



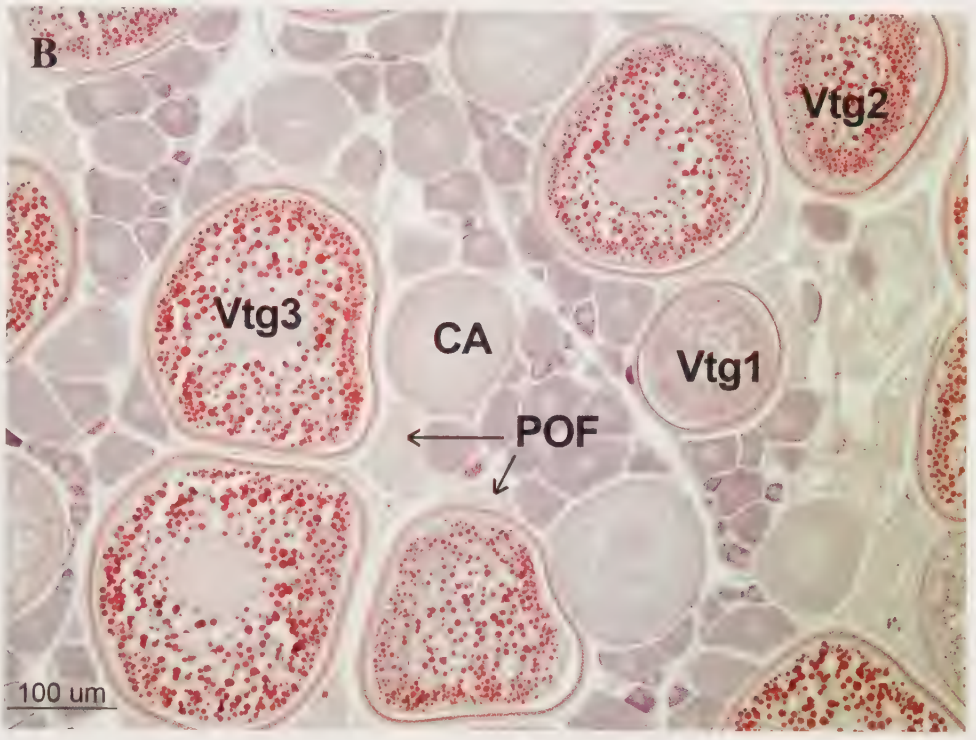


Figure 5

Gonadal development of Southern Kingfish (*Menticirrhus americanus*) sampled from the Mississippi Sound, Mississippi, from April 2008 to May 2009. (**A**) Plot of mean values in a gonadosomatic index for male and female Southern Kingfish (for sample sizes of each sex, see Table 1). Error bars indicate ±1 standard error; in several months the error bars for males, are hidden by the data point symbol. Data points are significantly different ($P \leq 0.05$) if letter labels are not the same. (**B**) Photomicrograph of a female Southern Kingfish in the spawning-capable phase. Labels indicate the following oocyte stages: cortical alveoli (CA), primary vitellogenic (Vtg1), secondary vitellogenic (Vtg2), tertiary vitellogenic (Vtg3), and postovulatory follicle complex (POF).

moderate maximum TL, age, RBF, duration of spawning season, and *b* values. Group E comprises fishes from all 3 regions: Spotted Seatrout (*Cynoscion nebulosus*) from Atlantic and GOM populations, as well as Weakfish (*Cynoscion regalis*), Spotfin Croaker (*Roncador stearnsii*), and Yellowfin Croaker (*Umbrina roncador*).

Discussion

In this article, we identify and address gaps in the understanding of the life history of the recreationally and commercially important Southern Kingfish in the northcentral GOM. We report that Southern Kingfish

Table 4

Seasonal spawning frequency for Southern Kingfish (*Menticirrhus americanus*) in the northcentral Gulf of Mexico determined with 2 histological methods. The postovulatory follicle (POF) method is based on the presence of POF ≤24 h and the oocyte maturation (OM) method is based on the presence of oocytes in OM. Only females in the spawning capable phase (including the actively spawning subphase) were used in this analysis. Samples were collected from Mississippi Sound, Mississippi, between April 2008 and May 2009.

Season	*n*	POF spawning frequency (days)	OM spawning frequency (days)
Early (April–May)	79	11.29	11.29
Mid (June–July)	70	3.50	5.83
Late (Aug.–Sept.)	59	19.67	5.36
Total (April–Sept.)	208	6.93	6.93

has a 6-month spawning period that occurs from spring to summer and that an individual female spawns, on average, 213.1 eggs g^{-1} OFBW once per week. Females reach sexual maturity at a relatively small size (171 mm TL) and young age (1+ years). We report significant differences in sex-specific length at age and weight at length. Finally, we document how the life-history traits of this species are part of the multivariate continuum of sciaenid stocks in the coastal waters of the continental United States.

Our analysis of the reproductive traits of the Southern Kingfish provided the timing of spawning through the use of both GSI and histological analysis, and we identified a single, extended spawning period. The spawning season for Southern Kingfish in the northcentral GOM begins in late March and ends in September, with peaks in male (1.56%) and female (4.75%) GSI values in April. Other investigators have previously reported similar spawning seasons for Southern Kingfish in both the Atlantic and GOM on the basis of macroscopic inspection of the ovary and GSI values (Hildebrand and Cable, 1934; Bearden, 1963; Lagarde[2]; Smith and Wenner, 1985; McDowell and Robillard, 2013). An extended spawning season (≥3 months) is characteristic of most sciaenid species (Appendix). Our analysis of this reproductive trait places Southern Kingfish in group B (see Fig. 7), a group partially characterized by having the longest spawning season.

Our finding of the existence of a single spawning season is in contrast to results from Harding and Chittenden (1987), who found on the basis of male and female GSI and macroscopic classification of maturity that the spawning period in the northwestern GOM occurred from February or March to November and comprised 2 primary, discrete spawning periods (spring and fall). However, the Harding and Chittenden (1987) collections were from the deeper part of the bathymetric range of Southern Kingfish; more thorough collections in estuaries, the surf zone, or the shallow inshore waters could resolve whether there are 2 discrete spawning periods, as they have suggested, or 1 spawning period with 2 periods of recruitment.

Although GSI values are typically good indicators of spawning preparedness, histological analysis can refine and more precisely delineate the spawning season and has not been previously performed for Southern Kingfish from the GOM. The spawning season estimated through our histological analysis matched our GSI results; spawning is initiated in April and ends in September. Additionally, there were fish in the spawning-capable phase in both March and October, although no females were in the actively spawning subphase during these months. Our estimate of the Southern Kingfish spawning period is supported by Anderson et al. (2012), who studied daily growth rings in otoliths from juveniles in the northcentral GOM and estimated birth dates with back calculation. Although there were fish in that study with

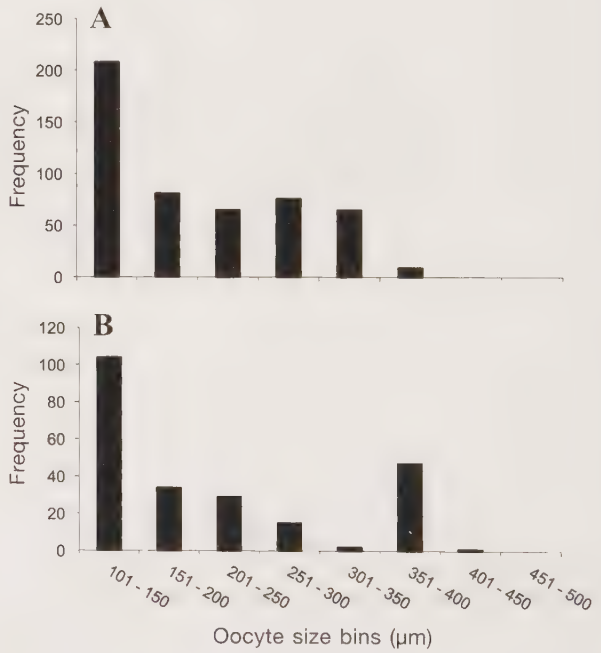


Figure 6

Oocyte size frequency distribution for Southern Kingfish (*Menticirrhus americanus*) collected from the Mississippi Sound, Mississippi, between April 2008 and May 2009 and found to be in the (**A**) spawning-capable phase or (**B**) actively spawning subphase.

Table 5

Mean batch fecundity (number of eggs) and relative batch fecundity (number of eggs per gram of ovary-free body weight) by month and age class for Southern Kingfish (*Menticirrhus americanus*) collected between April 2008 and May 2009 from the northcentral Gulf of Mexico (Mississippi Sound, Mississippi). Standard errors of the mean (SE) are provided in parentheses.

Month or age	*n*	Mean batch fecundity (SE)	Mean relative batch fecundity (SE)
May	2	33,944 (2408)	228.0 (25.1)
July	3	35,150 (12,213)	201.6 (18.9)
August	3	38,722 (20,888)	259.6 (124.9)
September	3	33,924 (12,544)	168.1 (70.3)
Age 1	4	33,730 (15,591)	235.7 (91.5)
Age 2	7	36,622 (6122)	200.2 (29.4)
Overall	11	35,571 (6405)	213.1 (35.7)

estimated birth dates in late March (n=5), the greatest frequencies occurred between June and August, and this period marks the plateau in GSI values and the highest percentages of actively spawning fish noted from histological analysis. This evidence indicates that the notion of 2 discrete spawning periods within the season does not apply to this population. Furthermore, our data are in close agreement with recent histological analyses of Southern Kingfish from the SAB, where this species also has a single spawning period. McDowell and Robilland (2013) found spawning fish in Georgia estuaries from March to July, although spawning-capable females were seen also in August and September.

Fecundity data provide information that will aid in the determination of the spawning potential of Southern Kingfish at different lengths and ages; however, fecundity measurements are poorly understood for the Southern Kingfish across its range. Previously reported estimates for 20 females in the northcentral GOM (Fritzsche and Crowe[3]) were a mean BF of 105,359 eggs (range: 46,024–332,229 eggs) and a mean RBF of 527 eggs g^{-1} OFBW, but these 2 estimates are based on all oocytes >300 µm. Our data show that vitellogenic oocytes between 300 and 350 µm do not undergo OM and, therefore, represent several potential batches. Batch fecundity estimates in our study were lower than those found by Fritzsche and Crowe[3] because only hydrated oocytes or those oocytes undergoing OM were used. Militelli et al. (2013) reported RBF estimates for 8 Southern Kingfish from Argentina as 217 eggs g^{-1} OFBW (SE 70)—a finding that is similar to our results of 231 eggs g^{-1} OFBW (SE 36) for fish in the northcentral GOM. McDowell and Robillard (2013) did not directly report RBF data for Southern Kingfish from Georgia, but we calculated RBF to be 308.6 eggs g^{-1} total weight (SE 27.6) on the basis of information in their manuscript.

The lack of a significant relationship in our data between BF or RBF and TL, OFBW, or age is unusual, but it may be linked to our small sample size and the potential for significant variation in fecundity among individuals within a protracted spawning season (Lowerre-Barbieri et al., 2009). McDowell and Robillard (2013) had a more robust sample size of 36 fish and found a significant relationship between batch fecundity and both length and weight. Therefore, our fecundity estimates should be viewed with caution, despite their similarity to fecundity estimates of the Argentinean stock. Overall, Southern Kingfish exhibit some of the lowest reported RBF values for sciaenids (Appendix), a trait shared with the other members of group B in the PCA (see Fig. 7): Sand Seatrout, White Croaker, and Queenfish.

Table 6

Summary of loadings from principal components analysis (PCA) of the 5 somatic and reproductive variables onto the 2 most meaningful principal components (PC 1 and PC 2). Loadings represent Pearson's correlations of original metrics to each component. Only correlation values $|\geq 0.60|$ (shown in bold) are considered useful for naming components (Hair et al., 1984). Maximum total length is presented in millimeters, duration of spawning season is shown in months, relative batch fecundity is reported in number of eggs per gram of ovary-free body weight and age at maturity is presented in years; b=slope of length-weight power function.

Variable	PC 1	PC 2
Maximum total length	**0.853**	−0.210
Spawning-season duration	−0.297	**0.830**
Relative batch fecundity	**−0.626**	−0.396
Age at maturity	**0.861**	−0.252
b	0.023	**0.708**

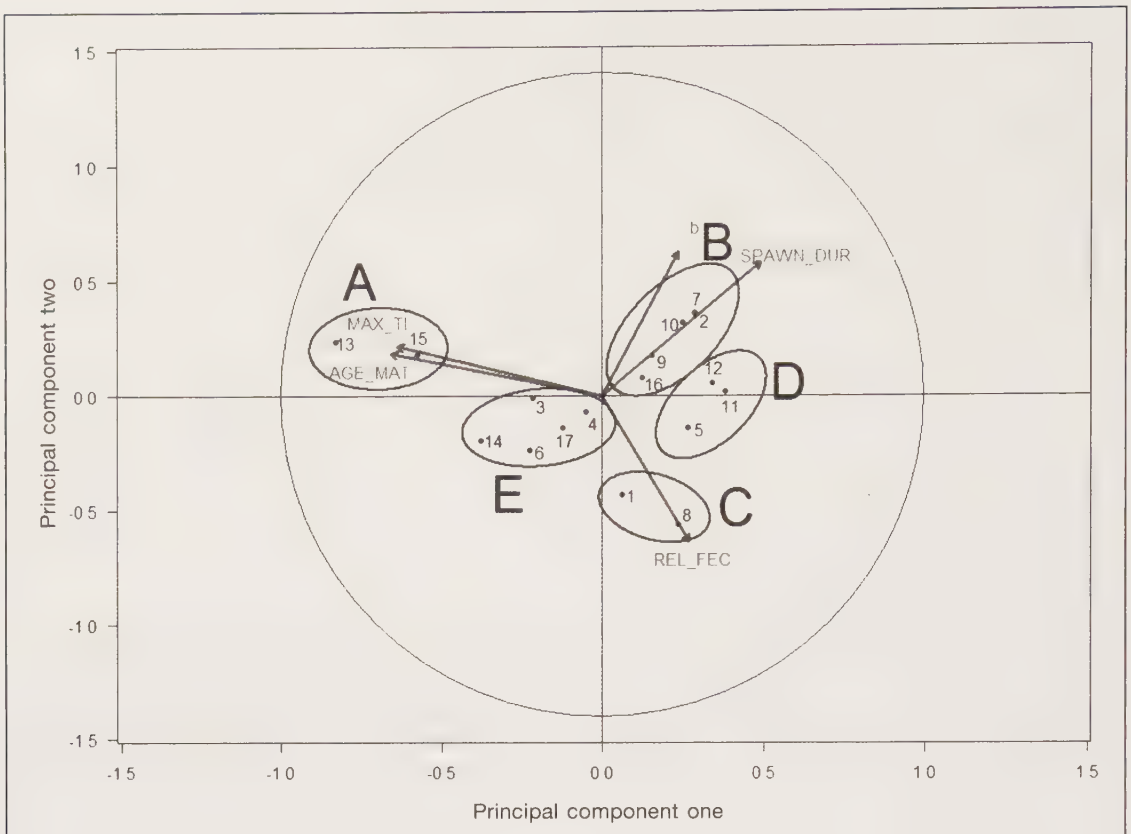


Figure 7

Biplot of first (43.3%) and second (25.0%) principal components from principal component analysis (PCA) on the basis of the relative measures—each denoted with an arrow—of reproductive traits (spawning-season duration [SPAWN_DUR], relative batch fecundity [REL_FEC], and age at maturity [AGE_MAT]) and somatic traits (maximum total length [MAX_TL] and the weight-at-length parameter [*b*]) for 17 populations of sciaenids in 3 regions: Gulf of Mexico (GOM), Pacific Ocean, and Atlantic Ocean. Numbered points indicate sciaenid populations: (1) GOM Silver Perch (*Bairdiella chrysoura*), (2) GOM Sand Seatrout (*Cynoscion arenarius*), (3) Atlantic Spotted Seatrout (*C. nebulosus*), (4) GOM Spotted Seatrout, (5) GOM Silver Seatrout (*C. nothus*), (6) Atlantic Weakfish (*C. regalis*), (7) Pacific White Croaker (*Genyonemus lineatus*), (8) GOM Spot (*Leiostomus xanthurus*), (9) Atlantic Southern Kingfish (*Menticirrhus americanus*), 10. GOM Southern Kingfish, (11) Atlantic Atlantic Croaker (*Micropogonias undulatus*), (12) GOM Atlantic Croaker, (13) GOM Black Drum (*Pogonias cromis*), (14) Pacific Spotfin Croaker (*Roncador stearnsii*), (15) GOM Red Drum (*Sciaenops ocellatus*), (16) Pacific Queenfish (*Seriphus politus*), and (17) Pacific Yellowfin Croaker (*Umbrina roncador*). The letters A–E indicate the 5 groups of sciaenids identified through PCA. The large circle represents a maximum correlation of 1 between original variables in the PCA analysis and the factor loadings for each variable that were generated by the PCA.

Spawning frequency for batch-spawning species like Southern Kingfish, when combined with batch fecundity, provides an estimate of the total annual reproductive output of a species. Histological confirmation of multiple spawnings per season for populations of Southern Kingfish in Brazil and the SAB have been reported recently on the basis of the appearance of POFs and surrounding oocytes in multiple stages of development (Haluch et al., 2011; McDowell and Robillard, 2013). In our study, the seasonal spawning frequency was found to be about 7 days between spawnings with a peak of 3–6 days (depending on method, POF or OM) during June and July in the northcentral GOM. This interspawning interval is one of the longest ones reported among the Sciaenidae (see Appendix) and contrasts with that of 2–4 days between spawnings for the SAB population of Southern Kingfish (McDowell and Robillard, 2013). However, spawning-frequency data are based on a 4-month spawning season in Georgia and a 6-month season in the GOM—a difference that may account for some of this variation.

Unfortunately, spawning-frequency data are available for only 11 of the 24 economically important sciaenid species or populations and, for that reason, were not included in the PCA of reproductive and somatic traits. Therefore, the importance of spawning frequency to the reproductive and somatic relationships between Southern Kingfish and other sciaenids is unknown.

The OM method appeared to be a reliable indicator of spawning frequency of Southern Kingfish in the GOM. Similarly, McDowell and Robillard (2013) used the OM method (specifically, presence of hydrated oocytes) to determine spawning frequency of Southern Kingfish from the SAB, although they did not present seasonal differences in spawning frequency. In our study, the OM method indicated that no significant difference existed between seasons as was observed with the POF method. The interspawning interval at the end of the season was longer when calculated by the POF method than when estimated with the OM method—a result that was likely due to a sampling bias. Fish that had finished spawning for the year may have moved out of the sample areas, whereas females that were still preparing to spawn remained in those areas. Therefore, fish that contained oocytes in the OM stage may have been more vulnerable to capture than fish with POFs. Similar differences in spawning frequency between methods were noted in the late season of Silver Perch (Grammer et al., 2009), where the OM method revealed an estimated 1.6 days between spawnings and the POF method indicated an estimated 16 days between spawnings. Although Grammer et al. (2009) stated their results may have been a function of low sample size (n=16), our study had a larger sample size (n=59) that should not have been a contributing factor to the large difference observed. Interestingly, on the basis of percentage of spawning fish captured (OM method), spawning frequency of Southern Kingfish from Georgia also was highest at the beginning of the reproductive season (March and April; McDowell and Robillard, 2013).

Female Southern Kingfish in the northcentral GOM reached sexual maturity as small as 163 mm TL, corresponding to 1 year of age. Females reached 50% maturity by 171 mm TL and 100% maturity by 211 mm TL, both at age 1. These results are consistent with reports from Smith and Wenner (1985), who estimated that females from the SAB reached TL_{50} at 192 mm TL at age 1 and TL_{100} at 230 mm TL, also at age 1. Recently, McDowell and Robillard (2013) have confirmed these estimates of TL_{50} (199 mm TL) and 50% maturity (1.1 years), indicating little change in the population of Southern Kingfish from the SAB over the past 25 years. Similarly, Haluch et al. (2011) reported female TL_{50} at 167 mm TL from the area of Santa Catarina, Brazil, with TL_{100} at 228 mm TL. In contrast, Militelli et al. (2013) found TL_{50} for females in the coastal zone of Buenos Aires, Argentina, to be 223 mm TL, although this result was based on a relatively small sample size (n=54). Harding and Chittenden (1987) noted TL_{100} at 250 mm TL (with few maturing, virgin fish past 220 mm TL) for fish in the northwestern GOM, providing further evidence that Southern Kingfish in the GOM reach sexual maturity by age 1. Many sciaenids have developed a strategy to mature in the first year of life (Waggy et al., 2006; see Appendix); 10 of the 17 species or populations analyzed in the PCA were in the low age-at-maturity quadrats of the plot (groups B, C, and D in Fig. 7).

Population-level characteristics, such as mortality rates and longevity, have been shown to correlate with individual growth parameters (Beverton and Holt, 1959; Lorenzen, 2005). Therefore, the somatic growth characteristics of Southern Kingfish discussed here provide a proxy for the determination of these characteristics that can aid in the management of the species. Our results indicate geographic differences in the maximum length and age of Southern Kingfish, as well as sex-specific differences in growth and condition.

The maximum length from our study (348 mm TL) is similar to the lengths reported by Bearden (1963) on the East Coast of the United States (338 mm TL) and by Harding and Chittenden (1987) for the northwestern GOM (345 mm TL), but this result is smaller than the maximum size of 404 mm TL (Smith and Wenner, 1985) and 419 mm TL (McDowell and Robillard, 2013) reported for fish off the Atlantic coast of the southeastern United States. In our study, males from the GOM were found to have a smaller mean size (211.2 mm TL) than that of females (238.5 mm TL). Sex-specific differences in maximum length also were reported by Harding and Chittenden (1987) and McDowell and Robillard (2013) for Southern Kingfish, and such differences are common for species in this family (Chao, 1995, 2002).

On the basis of annuli counts in sagittal otoliths, maximum age for both males and females in the northcentral GOM was 4+ years. The oldest reported Southern Kingfish was an individual that reached age 6 from the Atlantic coast of the southeastern United States (Smith and Wenner, 1985), although this age determination was made with scale annuli, which is less accurate than age determination from otoliths (VanderKooy, 2009). Recent aging of Southern Kingfish from Georgia with the use of otoliths revealed a maximum age of 5 years, with the majority of fish ≤age 3. The maximum age and sizes of Southern Kingfish estimated in this study provide additional evidence that this species is of a relatively small size and has a short life span. Many other sciaenids are typically relatively small and have a short life span (Waggy et al., 2006; see Appendix); 10 of the 17 stocks analyzed in the PCA were in the small maximum TL quadrants of the plot (groups B, C, and D in Fig. 7).

Annual ring formation in otoliths of Southern Kingfish occurred from April to May, a finding that differs from the reported marginal increments in scales by Smith and Wenner (1985), who found that the scale annulus was formed in the winter and early spring. However, analysis of otoliths from Southern Kingfish

collected in Georgia confirms that formation of annual growth rings occurs during April and May (McDowell and Robillard, 2013). The formation of the opaque annual ring has been attributed to several factors, including seasonal temperature changes, feeding patterns, wet and dry seasons, and reproductive cycles (Beckman and Wilson, 1995). On the basis of our results, formation of opaque rings in the GOM population appears to coincide with the peak of the spawning season during April–May.

Sciaenid life-history traits

Despite the fact that a number of sciaenid species are commercially and recreationally important in the continental United States, complete life-history information is available for only a small number of species. In particular, information on fecundity and spawning frequency is lacking for over half of the stocks listed in the Appendix. Such information about the reproductive traits of these stocks is one important component for understanding population dynamics (Cortés, 1998), and priority should be placed on obtaining this information for these commercially or recreationally important stocks.

All Sciaenidae exhibit some common life-history traits, such as indeterminate fecundity, batch spawning, relatively small pelagic eggs, and an estuarine-dependent juvenile phase (Chao, 2002). However, we analyzed the range for 5 reproductive and somatic traits with 2 principal component axes and explained 68.1% of the variation among species. This result is lower than the 91% total variation explained by Winemiller and Rose (1992) with analysis of 5 traits on 3 principal component axes for 147 fish species representing multiple families, but variation in life history is reduced when analyzing traits of species within a single family. Waggy et al. (2006) examined the relationships among 8 life-history variables in 11 sciaenid species occurring in the GOM and Caribbean and found that 2 principal components explained 86% of the variance, although several of the variables they included in their analysis were correlated. We have determined that the components of our analysis represent size-related aspects of life history (PC 1) and spawning season dynamics (PC 2), both of which combine somatic and reproductive traits. Winemiller and Rose (1992) and Waggy et al. (2006) identified similar components in their life-history analyses.

We identified 5 distinct sciaenid groups on the basis of the PCA analysis (see Fig. 7), indicating these groups of species are very similar to each other. The 2 largest sciaenids in the analysis, Red Drum and Black Drum from the GOM, compose group A and have similar life-history traits, but they spawn at different times of the year (Murphy and Taylor, 1990; Nieland and Wilson, 1993). In group B, Sand Seatrout and Southern Kingfish are both GOM species with similar sizes, spawning seasons, and spawning frequencies, but Sand Seatrout is a more pelagic species that spawns in the nearshore GOM (Shlossman and Chittenden, 1981), whereas Southern Kingfish tend to be benthic and estuarine spawners, on the basis of the common occurrence of young fish in estuaries (Anderson et al., 2012). The Atlantic population of Southern Kingfish also is included in this group, indicating that geographic differences among a single species, although present, do not result in changes in basic life-history strategies. The inclusion of White Croaker of the Pacific in this same group indicates similar strategies across widely spaced regions.

Group C consists of the species with the highest RBF, Spot and Silver Perch; both species occur in the GOM but have different spawning seasons and locations (Cowan and Shaw, 1988; Grammer et al., 2009) and therefore reduce potential competition among larvae. The GOM species Atlantic Croaker and Silver Seatrout are both in group D but have different spawning seasons (White and Chittenden, 1977; DeVries and Chittenden, 1982), and the Atlantic population of Atlantic Croaker is found in this same group. Within group E, the Atlantic congeners Spotted Seatrout and Weakfish and the Pacific species Spotfin Croaker, and Yellowfin Croaker have similar spawning seasons and habitats within regions (Brown, 1981; Lowerre-Barbieri et al., 1996a; Miller et al., 2009), indicating that life-history traits among this group are very similar. Geographic differences in life-history parameters between Atlantic and GOM Spotted Seatrout (Brown, 1981; Murphy and Taylor, 1994; Brown-Peterson, 2003) appear to be once again less important than overall life-history strategies.

For all 3 of the sciaenid species that have both Atlantic and GOM populations—the Southern Kingfish, Atlantic Croaker, and Spotted Seatrout— those populations are in the same groups as their conspecifics, but those 3 species are in 3 different life-history groups within the PCA. Therefore, the similarity of overall within-species life-history strategies appears to override observed differences in reproductive seasons with latitude (Brown-Peterson and Thomas, 1988; Conover, 1992).

Overall, the PCA results indicate that groups A and E can be characterized as having a periodic or *K* life-history strategy but that group C has an opportunistic or *r* strategy (sensu Winemiller and Rose, 1992). Groups B and D (8 species) do not fit classic definitions of life-history strategies, indicating that strategies of smaller sciaenids with low fecundity may be more susceptible to environmental or physiological variation than larger sciaenids with high fecundity. Indeed, the importance of behavioral and physiological factors should be considered when evaluating life-history variation (Ricklefs and Wikelsik, 2002) because some observed variations may be a result of physiological sensitivity or behavioral control mechanisms that are related to the environment.

Conclusions

We examined the somatic and reproductive life-history characteristics of Southern Kingfish and described how the parameters in this multivariate set relate to the parameters of other species of Sciaenidae that are encountered by recreational and commercial fisheries in the continental United States. This study shows that Southern Kingfish is a generally short-lived, early maturing fish with a longer spawning season than that of other Sciaenidae and that it exhibits significant sex-specific differences in somatic characteristics. The multivariate analysis that we used in this study also indicates that relationships of demographic characteristics within this family are complex. Such complexity is mediated by both evolutionary and ecological processes. Our inventory of life-history characteristics of sciaenid species indicates a number of gaps in available data. Demographic data that are missing or that are collected and reported but that are not sex specific may, to some extent, compromise the use of among-population comparisons.

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Appendix

Table of sciaenid species in the U.S. Exclusive Economic Zone and life history metrics used in this study. An asterisk (*) indicates that values are reported for Gulf of Mexico (GOM) and Atlantic stocks combined. TL=total length, FL=fork length, SL=standard length, F=female, p=pooled, mo=months, y=years. Morphology Index (*b*) is defined as the exponent of weight at length from the power function. A dash alone indicates that no data were available. The species include White Seabass (*Atractoscion nobilis*), Silver Perch (*Bairdiella chrysoura*), Black Croaker (*Cheilotrema saturnum*), Sand Seatrout (*Cynoscion arenarius*), Spotted Seatrout (*Cynoscion nebulosus*), Silver Seatrout (*Cynoscion nothus*), Shortfin Corvina (*Cynoscion parvipinnis*), Weakfish (*Cynoscion regalis*), White Croaker (*Genyonemus lineatus*), Spot (*Leiostomus xanthurus*), Southern Kingfish (*Menticirrhus americanus*), Gulf Kingfish (*Menticirrhus littoralis*), Northern Kingfish (*Menticirrhus saxatilis*), California Corbina (*Menticirrhus undulatus*), Atlantic Croaker (*Micropogonias undulatus*), Black Drum (*Pogonias cromis*), Spotfin Croaker (*Roncador stearnsi*), Red Drum (*Sciaenops ocellatus*), Queenfish (*Seriphus politus*), and Yellowfin Croaker (*Umbrina roncador*). x=mean value.

Species	Region	Max age (y)	Max length (TL_∞) (mm TL)	Spawning-season duration (mo)	Spawning frequency (d)	Relative fecundity (eggs g^{-1} ovary-free body weight)	Age at maturity (y)	Size at maturity (mm)	Morphology index (*b*)	References
White Seabass	Pacific	20	1660	6–8	–	–	4	610 TL	2.94	7,22,41,44
Silver Perch	GOM	4–5	250	3	1.3–1.6	863	0+	110–120 TL	2.93 (F)	8,21
Black Croaker	Pacific	21	394	5	–	–	1+	182 TL	2.92	20,30
Sand Seatrout [a]	GOM	3	(574)	7	2.8	348	0+ to 1	147 SL	3.08 to 3.24 (F)	16,42,43
Spotted Seatrout	Atlantic	15	796 (854)	3–5	3.2–6.5	319	1–2	280–350 TL	2.99 (F)	5,6,34
	GOM	9	712 (817)	6–6.5	2.6–5	250–650	1	245–285 TL	2.86 (F)	6,34,36
Silver Seatrout	GOM	1.5	380	5.5	–	878	0+	123–164 TL	3.01(p)	13,42
Shortfin Corvina	Pacific	–	690	–	–	–	–	–	3.00	23
Weakfish	Atlantic	8	950	3.5	2.6–12.6	375–880	1	170 TL	2.86 to 2.98	27, 28, 37
White Croaker	Pacific	13–15	410–432	7–10	5	19–180	1	130–150 TL	2.94	19,22,26,41
Spot	GOM	2–3, 5	250	5	–	267–2948 (x=1607)	1+	127 TL	2.95 (p)	10,38,42
Southern Kingfish	Atlantic	5	418.9 (F) 290.7 (M)	6	2.0–4.2	309	1.1	199 TL	3.13 [b,c]	29
	GOM	4+	348 (303)	6	6.9	231	1	171 TL	3.17 (F)	This study
Gulf Kingfish	*	2	483	4	–	–	–	210 TL	2.87(p)	1, 23
Northern Kingfish	*	4	450–500	–	–	–	1	186–230 TL	3.08(p)	1
California Corbina	Pacific	8	710	5	–	–	3 (F)	325 TL	3.07 (p)	17,24,41
Atlantic Croaker	Atlantic	7	521	6	–	1240–1818 (x=1529)	1+	173 TL	3.23 (p)	2,32,40
	GOM	3–5, 8	369	4–8	–	519–1581 (x=1050)	1+	140–170 TL	3.14 (p) or 2.87(p)	3,10,14,15,25, 38,42,45
Black Drum	GOM	43	1500	2, 4	3–4	67–793	5	600–649 FL	3.05 (p)	4,18,33, 35
Spotfin Croaker [d]	Pacific	24	675–700	4	–	545	3 (F)	312 TL	2.94 (p)	7,24,31,46
Red Drum	Atlantic	33	1119	3	–	–	6	900 TL	3.03 (F)	33
	GOM	24	992	3	2–4	42–447	4	700 TL	3.10 (F)	9,33,47

Appendix continued

Queenfish [d]	Pacific	12	(198)	6	7.4	264–366	2	106–110 SL	2.85 to 3.15	11,12,19
Yellowfin Croaker [d]	Pacific	15	560 (313)-F	3	–	489	1.5 (F)	140 SL	3.02	31,39

Key to references: 1=Armstrong and Muller, 1996; 2=Barbieri et al., 1994; 3=Barger, 1985; 4=Beckman et al., 1990; 5=Brown, 1981; 6=Brown-Peterson, 2003; 7=**Chao, 1995**; 8=Chavance et al., 1984; 9=Comyns et al., 1991; 10=Cowan and Shaw, 1988; 11=DeMartini, 1990; 12=DeMartini and Fountain, 1981; 13=DeVries and Chittenden, 1982; 14=Ditty, 1986; 15=Ditty et al., 1988; 16=Ditty et al., 1991; 17=Eschmeyer et al., 1983; 18=Fitzhugh et al., 1993; 19=Goldberg, 1976; 20=Goldberg, 1981; 21=Grammer et al., 2009; **22=Hart, 1973**; 23=Joseph, 1962; 24=Kobylanski and Sheridan, 1979; 25=**Love et al., 1984**; 26=Lowerre-Barbieri et al., 1996a; 27=Lowerre-Barbieri et al., 1996b; 28=McDowell and Robillard, 2013; 29=Miller et al., 2008; 30=Miller et al., 2009; 31=Morse, 1980; 32=Murphy and Taylor, 1990; 33=Murphy and Taylor, 1994; 34=Nieland and Wilson, 1993; 35=Nieland et al., 2002; 36=Nye and Targett, 2008; 37=Pattillo et al., 1997; 38=Pondella et al., 2008; 39=Ross 1988; 40=**Shanks and Eckert, 2005**; 41=Sheridan et al., 1984; 42=Shlossman and Chittenden, 1981; 43=**Thomas, 1968**; 44=White and Chittenden, 1977; 45=Williams et al., 2012; 46=Wilson and Nieland, 1994.

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Seasonal distribution and abundance of cetaceans off Southern California estimated from CalCOFI cruise data from 2004 to 2008

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Abstract—Documenting year-round diversity and distribution of marine mammals off Southern California is important for assessment of effects of potentially harmful anthropogenic activities. Although the waters off Southern California have been surveyed extensively for marine mammals over the past 18 years, such surveys have been periodic and were conducted primarily from summer to fall, thereby missing potential seasonal shifts. We examined seasonal abundance and population density of cetaceans off Southern California from 16 shipboard line-transect surveys conducted quarterly during 2004–08. The study area consisted of 238,494 km^2 of coastal, shelf, and pelagic oceanic habitat from nearshore waters to 700 km offshore. Based on 693 encounters of 20 cetacean species, abundance estimates by seasonal period (summer–fall or winter–spring) and depth (shallow: <2000.5 m; deep: ≥2000.5 m) were determined for the 11 most commonly encountered species. The following are values of uncorrected density (individuals/1000 km^2, coefficients of variation in parentheses) for the seasonal period and depth with greatest density for a selection of the species in this study: blue whale (*Balaenoptera musculus*), summer–fall, shallow, 3.2 (0.26); fin whale (B. physalus), summer–fall, shallow, 3.7 (0.30); humpback whale (*Megaptera novaeangliae*), summer–fall, shallow, 3.1 (0.36); short-beaked common dolphin (*Delphinus delphis*), summer–fall, shallow, 1319.7 (0.24); long-beaked common dolphin (*D. capensis*), summer–fall, shallow, 687.9 (0.52); and Dall's porpoise (*Phocoenoides dalli*), winter–spring, deep, 48.65 (0.28). Seasonally, density varied significantly by depth for humpback whales, fin whales, and Pacific white-sided dolphins.

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At least 30 species of cetaceans are found in the California Current (Leatherwood et al., 1982), including 5 species of large whales listed as endangered under the U.S. Endangered Species Act. The abundance and diversity of species along the West Coast of the United States and the continental slope are closely linked to the high level of biological production that is caused by upwelling and mixing of 4 different water masses along the California coast on a seasonal and interannual basis (Reid et al., 1958; Smith et al., 1986; Munger et al., 2009). Although these waters are important to marine fauna, they are also increasingly important to humans who use them for commercial shipping and fishing; oil and gas exploration, development, and production; naval exercises; and recreation. The combined use of these highly productive waters by cetaceans and humans can lead to ships striking large whales (Jensen and Silber, 2003; Berman-Kowalewski et al., 2010), entanglements of cetaceans in fishing gear (Julian and Beeson, 1998; Laist et al., 2001; Carretta et al., 2011b), and disruption of normal behaviors by underwater sound (McDonald et al., 2006; Weilgart, 2007). To assess long-term impacts of fisheries, industry, and ecosystem variability on marine mammals, it is necessary to estimate abundance, understand stock structure, and determine seasonal habitat use by the species that inhabit these waters.

Abundance for the summer and fall seasons has been estimated for many cetacean species in waters off California, Oregon, and Washington through the use of ship-based line-transect surveys or mark-recapture techniques of photographically identified whales (Calambokidis and Barlow, 2004; Barlow and Forney, 2007; Carretta et al., 2011b). However, weather conditions make ship-based line-transect surveys difficult to conduct year-round, and few studies have quantified habitat and distribution shifts of marine mammals during the

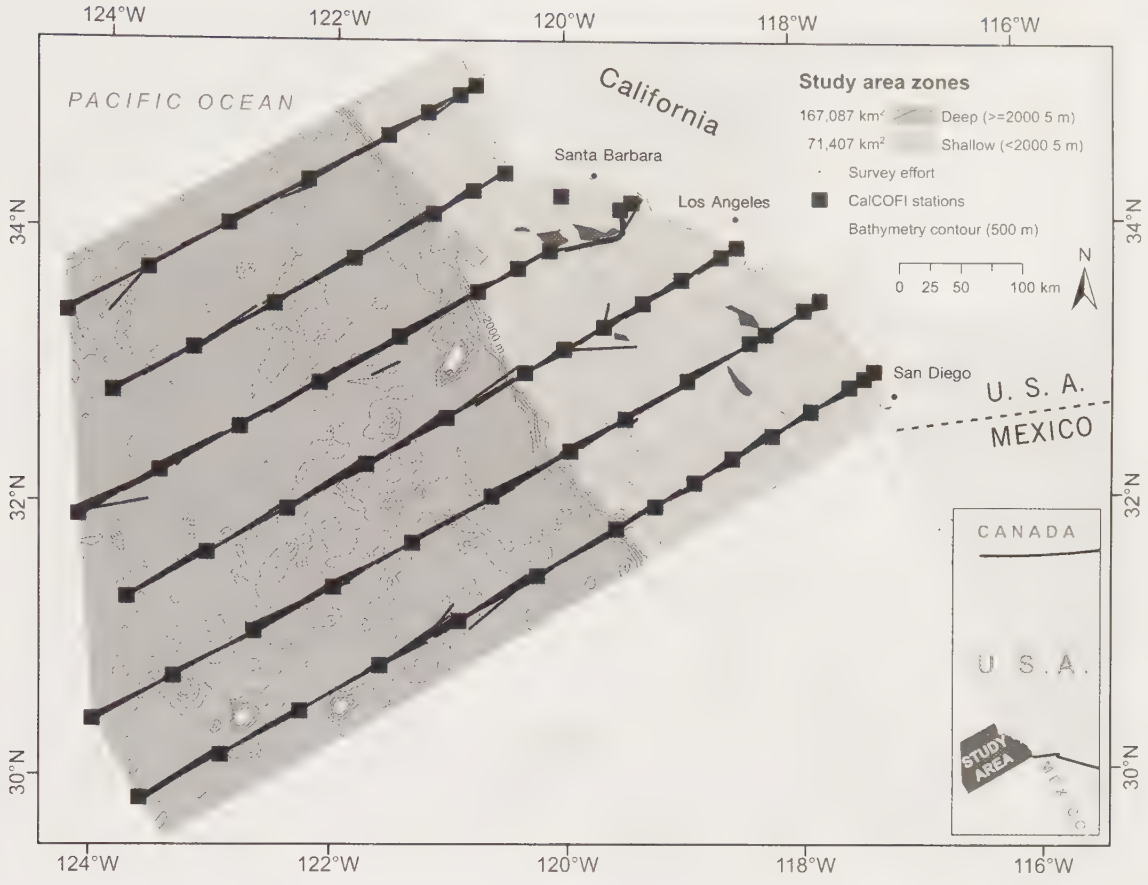

Figure 1

Map of the study area and 6 southern transect lines of 16 quarterly California Cooperative Oceanic Fisheries Investigation (CalCOFI) surveys conducted from July 2004 to April 2008 off Southern California. Shallow survey area (<2000.5 m) is lighter gray and deep survey area (≥2000.5 m) is dark gray. Dark squares on CalCOFI transect lines indicate oceanographic sampling stations. The CalCOFI study area (238,494 km^2) occurs completely inside the larger southern stratum (318,500 km^2) of the Southwest Fisheries Science Center shipboard surveys that extends farther to the northwest.

winter and spring months (Dohl et al.[1]; Forney and Barlow, 1998; Becker, 2007). In this study, new estimates of cetacean abundance were calculated off Southern California with marine mammal sighting data collected during 16 cruises undertaken as part of the California Cooperative Oceanic Fisheries Investigation (CalCOFI) (Bograd et al., 2003; Ohman and Venrick, 2003; Soldevilla et al., 2006). Marine mammal surveys on CalCOFI cruises are conducted quarterly, along predetermined transect lines between oceanographic water sampling stations (Fig. 1). The depth of the study area is extremely variable, with shallow waters inshore of the Channel Islands, a steep slope west of these islands, and an expansive deepwater plain offshore. Almost 30% of CalCOFI transect lines occur in water depths of 20–2000 m, and 69% of them occur in water depths of 3001–4600 m, and there is minimal (1%) coverage with transect lines in water depths of 2001–3000 m owing to the steep slope and orientation of the transect lines. Therefore, this study provides information on seasonal and interannual presence of cetaceans in both coastal and deep offshore waters. Such information is important to understanding and potentially mitigating effects of human activities on cetacean populations off Southern California.

Materials and methods

Data collection

Dedicated visual observers conducted line-transect surveys for marine mammals (Buckland et al., 1993; Kinzey and Gerrodette, 2003) during 16 quarterly Cal-

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Table 1

Individual cruise identification, vessel, schedule (beginning, ending, season), line-transect-survey effort in kilometers, and marine mammal visual observers of 16 California Cooperative Oceanic Fisheries Investigation (CalCOFI) surveys conducted from July 2004 to April 2008. Height of observer platform on the 3 research vessels from which these surveys were completed: 13.2 m on RV *Roger Revelle* [RR], 8.1 m on RV *New Horizon* [NH], and 11.0 m on NOAA Ship *David Starr Jordan* [DSJ].

CalCOFI cruise ID	Vessel	Begin	End	Season	Survey effort (km)	Visual observers[1]
0407JD	DSJ	13-Jul-2004	28-Jul-2004	Summer	1543	RWB, ABD
0411RR	RR	2-Nov-2004	19-Nov-2004	Fall	1295	ABD, AM, MS, SEY
0501NH	NH	4-Jan-2005	20-Jan-2005	Winter	1006	DLC, EV
0504NH	NH	15-Apr-2005	30-Apr-2005	Spring	1485	DLC, SMC
0507NH	NH	1-Jul-2005	16-Jul-2005	Summer	1571	DLC, ABD, VI
0511NH	NH	4-Nov-2005	20-Nov-2005	Fall	1104	DLC, SMC
0602JD	DSJ	4-Feb-2006	25-Feb-2006	Winter	1144	GSC, SMC
0604NH	NH	1-Apr-2006	17-Apr-2006	Spring	1624	DLC, ABD
0607NH	NH	8-Jul-2006	24-Jul-2006	Summer	1595	DLC, AMH
0610RR	RR	21-Oct-2006	5-Nov-2006	Fall	1208	ABD, AMH
0701JD	DSJ	12-Jan-2007	2-Feb-2007	Winter	1080	GSC, ABD
0704JD	DSJ	28-Mar-2007	18-Apr-2007	Spring	911	GSC, SMC
0707NH	NH	28-Jun-2007	13-Jul-2007	Summer	1502	AMH, SEY
0711NH	NH	02-Nov-2007	18-Nov-2007	Fall	1109	DLC, LJM
0801JD	DSJ	07-Jan-2008	23-Jan-2008	Winter	935	DLC, GSC
0803JD	DSJ	24-Mar-2008	09-Apr-2008	Spring	884	DLC, GSC

[1]Observers: R. W. Baird, D. L. Camacho, G. S. Campbell, S. M. Claussen, A. B. Douglas, A. M. Havron, V. Iriarte, A. Miller, L. J. Morse, M. Smith, E. Vazquez, and S. E. Yin.

COFI cruises from July 2004 to April 2008 (Table 1). Covering an area of 238,494 km^2, the study area consisted of coastal, shelf, and pelagic oceanic habitat from nearshore waters to waters 700 km offshore and up to 4600 m deep. Observers used unaided eye or handheld 7×50 reticle Fujinon[2] binoculars (Fujifilm Corp., Tokyo) to sight, identify, and estimate group sizes of cetaceans and pinnipeds encountered along the transect lines between CalCOFI hydrographic sampling stations (Fig. 1). The Southern California hydrographic sampling station sites are set along 6 parallel lines running southwest to northeast, with lines increasing in length from north to south (470–700 km). Stations occur every 37 km in coastal and continental shelf waters and every 74 km in offshore locations (Fig. 1). Occasionally, transect lines were interrupted by naval activity or adverse weather conditions; in these cases, the observers discontinued effort until their vessel adjusted to a course that intersected with the interrupted transect line. Transit lines that ran along the CalCOFI transect lines, as well as to and from the study area, were surveyed opportunistically in addition to the primary transect lines; however, these data were excluded from the analyses and results described here. Five northern lines were surveyed partially during 2 winter cruises; however, only a few sections of these lines were surveyed with acceptable sea conditions, and therefore these data also have been excluded from the analyses and results in this study.

Three vessels were used for the line-transect surveys: the RV *Roger Revelle* (2 surveys) and RV *New Horizon* (8 surveys) of the Scripps Institution of Oceanography, University of California, San Diego, and the NOAA Ship *David Starr Jordan* (6 surveys) (Table 1). Survey speeds ranged from 18.5 to 22.2 km/h. Height of the observer platform varied by vessel from 8.1 to 13.2 m, raising the possibility that there would be a vessel or a vessel-season bias. To test these biases, we ran single-factor analyses of variance (ANOVAs) to determine whether visual observers made initial sightings at significantly different distances for each vessel or vessel-season combination. Additionally, we ran tests to determine whether the number of transect line kilometers surveyed in good weather varied by season.

Scanning from directly abeam to 10° past the bow on either side of the vessel, 2 observers recorded marine mammal sightings. During 2 survey cruises, an additional person was available to record data and provide relief for observers at meal times (Table 1). Recorded sighting data included date, time, vessel latitude and longitude, vessel true heading, distance of animal from the vessel, sighting angle, θ, from the transect line, de-

[2] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

termined with an angle board (zero at bow, negative to port, positive to starboard), sighting number, species, group-size estimate (best, high, low), presence of calves, general behavior of animals, photographs (if taken), and comments pertaining to the sighting. Because of the surfacing behavior of cetaceans and lack of visibility while submerged, animal counts were only estimates, with the recorded "low" estimate being the minimum number of individuals observed during the sighting, the "high" estimate being the maximum, and the "best" estimate was always recognized as the value closest to the actual number of individuals. Group-size estimates and species confirmation were generally made by the lead observer but were agreed upon by all observers present.

Transect lines were surveyed in "passing mode," which does not allow for any alteration of course for closer examination of groups encountered. Barlow[3] stated that surveys conducted in passing mode yield less biased estimates of encounter rates but result in a higher number of unidentified groups and more biased estimates of group size and species percentages compared with surveys conducted in closing mode. Closing mode allows for all observers to go "off effort" and to adjust the course and speed of the vessel in order to approach animals sighted at a distance from the transect line. To assist with species identification and group-size estimation, 25× binoculars were available for all surveys on the *Roger Revelle*, for most surveys on the *David Starr Jordan*, and occasionally on the *New Horizon*. The 25× binoculars were used only as an aid once a group had been located with the naked eye or 7×50 binoculars to maintain a consistent search method between surveys.

Observers recorded effort (on or off), weather (sea state, swell height, visibility [or estimated distance that observers can detect a small cetacean], and precipitation), changes in course and speed, and sighting information onto data sheets. Observations were considered on effort if observers were actively searching with the unaided eye and 7×50 binoculars in a sea state 0–5, the vessel was traveling no less than 6 km/h, and there was a minimum visibility of 0.9 km (0.5 nmi) in front of the vessel. All sightings of all species of marine mammals were recorded with the exception of California sea lions (*Zalophus californianus*), which were sighted most often near the coast because estimation of group size and documentation of sighting details of high numbers of California sea lions in coastal waters would have compromised the ability of observers to sight and record other species that occur in the same area.

Because these surveys were conducted in passing mode and with limited use of 25× binoculars, some common dolphins (*Delphinus* sp.) that were encountered could be confirmed only to the genus level. Short-beaked common dolphins (*D. delphis*) and long-beaked common dolphins (*D. capensis*) have very similar morphological features and pigmentation, and they are difficult to distinguish at a distance (Rosel et al., 1994); therefore, observers were encouraged to obtain photographs if there was doubt about the identification of these or other species. Photographs were reviewed onboard, compared with identification guides (Reeves et al., 2002), and occasionally shared with experienced colleagues for species confirmation. Additionally, there are 2 forms of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) along the coast of California (Walker et al., 1986; Lux et al., 1997; Soldevilla et al., 2011); because these forms are indistinguishable from a distance, density and abundance for this species likely includes both forms.

Analytical methods

Sighting and effort data from the 16 CalCOFI cruises were split into 2 effort categories: 1) on-effort sightings on the 6 CalCOFI transect lines, the sightings that form the basis of all analyses and findings; and 2) opportunistic effort (sightings made off effort or when a vessel was not on a CalCOFI transect line), which is presented to show species diversity and presence or absence of species. We calculated encounter rates by season (number of on-effort sightings per 1000 km of transect line surveyed) for each species with 10 or more sightings. Distance r of the animal(s) sighted from the vessel and sighting position were determined from the reticle value (or estimated distance), height of observer platform, sighting angle (Δ) to animal from the bow of the vessel, and position of the vessel. To characterize the depth distribution of effort, sample points were created at 1-km intervals along transect lines within ArcGIS (vers. 9.2; Esri, Redlands, CA).

Sighting data also were plotted in ArcGIS, with sighting and effort data linked to a coastline shapefile and bathymetry data set from the ETOPO1 global relief model (Amante and Eakins, 2009) with 1850-m resolution (National Geophysical Data Center [NGDC], http://www.ngdc.noaa.gov/mgg/global/global.html); where highest resolution was not available from ETOPO1, the NGDC coastal relief model (NGDC, http://www.ngdc.noaa.gov/mgg/coastal/crm.html) provided 90-m resolution (73% of sighting depths and 49% of effort depths came from the 90-m resolution data set). Distance to the closest point of land, distance to the mainland, depth, and distance to the shelf break (200-m isobath) were also calculated for each sighting and effort location.

Using the cold (winter–spring, defined as January–April) and warm (summer–fall, defined as July–November) water distinctions in Forney and Barlow (1998), we tested for differences between the number of encounters of each positively identified species by

[3] Barlow, J. 1997. Preliminary estimates of cetacean abundance off California, Oregon, and Washington based on a 1996 ship survey and comparisons of passing and closing modes. Southwest Fish. Sci. Cent. Admin. Rep. LJ-97-11, 25 p.

Table 2

Covariates and summary statistics for the best-fit detection function models by species group from analyses of data from line-transect surveys conducted off Southern California from 2004 to 2008. The distribution of perpendicular sighting distances for pooled species was used to parameterize the detection function models summarized here, where $f(0)$ is the probability density function evaluated at a perpendicular distance of zero, bin width (m) is the interval chosen to show the fraction of probability distribution, truncation value excludes the 5% of sightings by species group that were farthest from the transect line and therefore considered outliers, ESW is the effective strip (half)width for which the number of groups outside the ESW is equal to the number missed inside the ESW, and CV is the coefficient of variation. The hazard-rate key function was used in the best-fit model for all species groups. Species groups were selected on the basis of factors that influence sightability, such as common school sizes, body shape, and behavior. The species group of large whales consisted of the blue, fin, humpback, sperm, and killer whales. Delphinids included the short- and long-beaked common, northern right whale, Pacific white-sided, Risso's, and bottlenose dolphins and the Dall's porpoise. For detection function plots, see Figure 2.

Species groups for estimating $f(0)$	Number of observations	Covariates	Bin width (m)	Truncation (m)	Average ESW (m)	CV
Large whales	127	Perpendicular distance	500	2348	1294	0.11
Delphinids	211	Perpendicular distance, sea state, species, log(group size)	100	1098	298	0.10
Dall's porpoise	48	Perpendicular distance, sea state	100	1098	305	0.22

seasonal period (winter–spring and summer–fall) and between the distance from shore and depth by the season, with Systat (vers. 13; Systat Software, Chicago, IL). Because our data had a bimodal distribution, Kruskal-Wallis one-way ANOVAs and Mann-Whitney *U*-tests were run to examine variation in encounters by habitat, year, and season with Minitab software (vers. 15.1.30; Minitab, State College, PA).

We used line-transect methods (Buckland et al., 2001) with multiple covariates (Marques and Buckland, 2003) to estimate cetacean abundance for 2 seasonal periods and 2 depth categories (defined below) in Distance software (vers. 6.0; Research Unit for Wildlife Population Assessment, University of St. Andrews, UK; Thomas et al., 2010). Distance software uses the perpendicular distance of the encounter to the transect line rather than the straight line distance (observer to animal) made at the time of the sighting; therefore, we calculated perpendicular distance as $r \sin \theta$ before uploading these data into Distance. Small sample size by season precluded our ability to estimate abundance quarterly; therefore, we estimated abundance within 4 strata in the study area. The strata were defined by 2 seasonal periods, winter–spring (cold water) or summer–fall (warm water), and 2 depth categories, shallow (<2000.5 m and deep (≥2000.5 m). On the basis of known ecological differences between shelf or slope and basin, with greater density of cetaceans near the coast, we chose to look at these data in 2 depth categories. Additionally, a histogram of effort as a function of depth showed that depth in our study area was strongly bimodal and that the depth of 2000.5 m was an appropriate cutoff point. Sample units were specified by survey number, line number, season, and depth to ensure that each of the 6 transect lines from each survey would be divided into a shallow and a deep sample unit.

To estimate density and abundance for a species, it is necessary to reliably estimate the detection function (the probability of seeing an animal at x distance from the transect line), and that requires a relatively large sample size (Buckland et al., 2001). The necessary sample sizes were not available for all species in this study; therefore, we pooled multiple species with similar surfacing characteristics (Barlow et al., 2001) and pooled (binned) sightings across season-and-depth strata to estimate the detection function (Table 2, Fig. 2). Pooled species groups were defined as 1) large whales, which included blue (*Balaenoptera musculus*), fin (*Balaenoptera physalus*), humpback (*Megaptera novaeangliae*), sperm (*Physeter macrocephalus*), and killer whales (*Orcinus orca*); 2) delphinids, which included short- and long-beaked common, northern right whale (*Lissodelphis borealis*), Pacific white-sided, Risso's (*Grampus griseus*), and common bottlenose (*Tursiops truncatus*) dolphins; and 3) Dall's porpoises (*Phocoenoides dalli*). Beaked whales and several other species of delphinids were encountered too infrequently to estimate abundance. Cetaceans that could not be identified to genus and species levels were not included in the pooled species groups for estimation of the detection function, and density and abundance levels were not estimated for them.

Potential covariates for building the detection function models included group size (a categorical variable that denotes whether sightings were greater or less than 20 individuals), cluster size (best estimate of group size), sea state (a numerical variable of 0–5), vessel, and species. Cut off points for group size were based on obvious breaks in histograms of group size for each species cat-

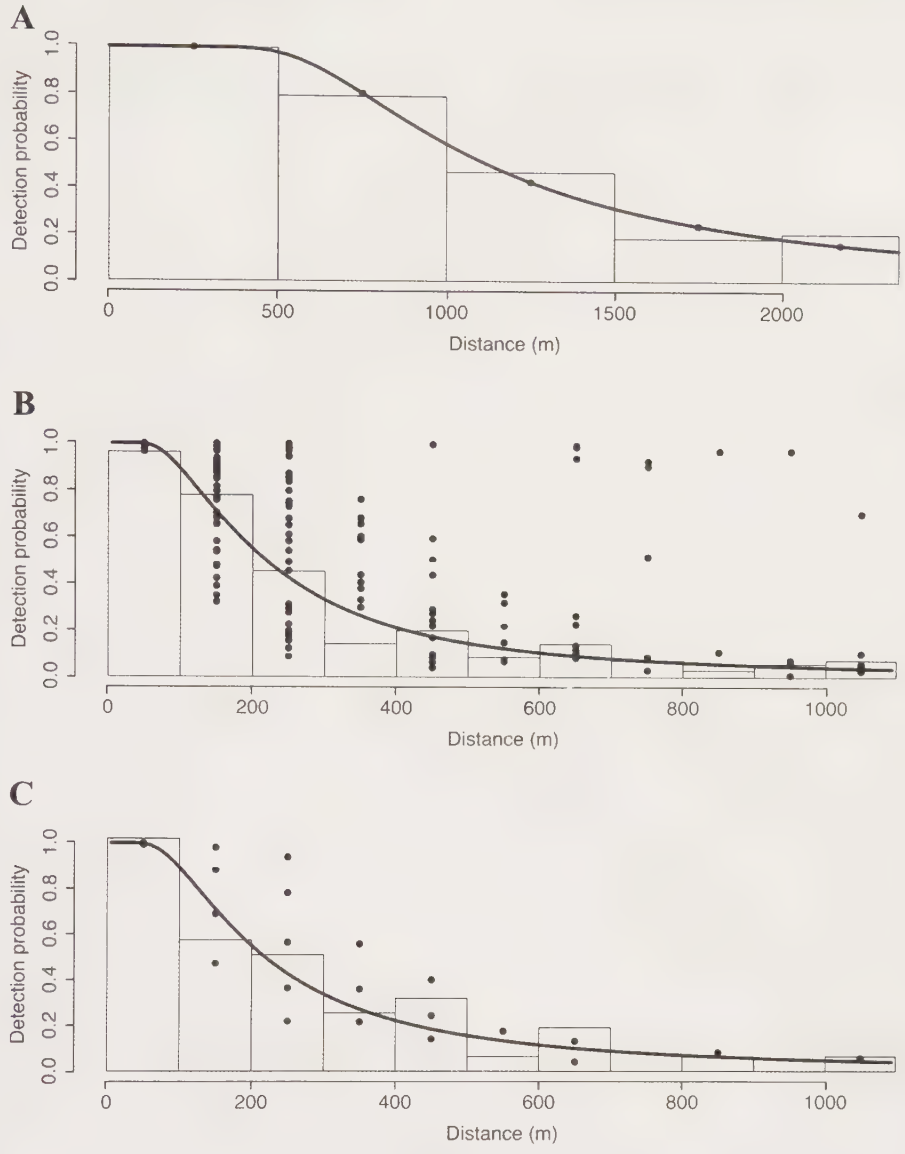

Figure 2

Detection function plots by species group ([**A**] large whales, [**B**] delphinids, and [**C**] Dall's porpoise [*Phocoenoides dalli*]) were created to visualize the correct detection functions to estimate density and abundance for the species most commonly encountered in the study area for line-transect surveys conducted off Southern California in 2004–08 during 16 quarterly California Cooperative Oceanic Fisheries Investigation cruises. The points are the probability of detection for each encounter dependent on its perpendicular distance and chosen covariate(s) for the best fit. The sighting data showed some evidence of heaping (i.e., rounding to certain distances) because of the limitations of the use of reticles to estimate distance. Therefore, sightings were binned to facilitate data analysis (Buckland et al., 2001). For detection function covariates and summary statistics, see Table 2.

egory. Selection of a detection function model was based primarily on the Akaike's information criterion (AIC) value (generated with Distance) and then confirmed by visual examination of detection plots (Burnham and Anderson, 2002). Half-normal and hazard-rate key functions often provide a good fit to data used to model detection functions (Thomas et al., 2010). Although both were considered in the models tested, the hazard-rate

model was chosen for all 3 groups on the basis of AIC values and visual inspection (Thomas et al., 2010).

Line-transect theory assumes that the probability of detecting an animal on the transect line, $g(0)$ equals 1.0 (perfect detectability), although this assumption is rarely true for marine mammals and can be relaxed if a correction factor is estimated. Estimation of a correction factor was beyond the scope of this study, and $g(0)$ is assumed to equal 1.0 and to be constant across sea states. The 5% of sightings made at the greatest distances to the vessel were assumed to be outliers and were truncated to improve the ability to fit the probability density function $f(0)$ (Buckland et al., 2001). Truncation distance was 2348 m for large whales and 1098 m for delphinids and porpoises. There were 7 whale, 11 dolphin, and 2 porpoise sightings recorded beyond the truncation distance and these were excluded from density and abundance analyses. We calculated density, D_i, for a given species within the study area i as

$$D_i = \frac{1}{2L_i} \sum_{j=1}^{n_i} \frac{f(0|z_j) * s_j}{g_j(0)}, \quad (1)$$

where L_i = the length of on-effort transect lines within the study area I;
$f(0|z_j)$ = the probability density function at zero with associated covariates z for group;
s_j = the number of individuals of that species in group j;
$g_j(0)$ = the transect line detection probability of group j; and
n = the number of groups of that species encountered in the study area i.

Group abundance for each species in each stratum was estimated as

$$\widehat{N_G} = \frac{A}{2wL} \sum_{i=1}^{n} \frac{1}{\widehat{P_1}}, \quad (2)$$

where A = the area of the stratum;
L = the total search effort in the stratum;
n = the number of unique groups;
w = the truncation distance by species group; and
$\widehat{P_1}$ = the estimated probability of detecting group i obtained from the fitted detection model.

Results

Survey effort and sightings

Line-transect surveys were conducted during 16 cruises over 5 years, with 3 years of 4-season effort and 2 years of 2-season effort (Table 1). Including all survey effort from the southern CalCOFI transect lines, observers collected visual data on marine mammals over 267 days and searched 25,079 km of transect lines. Of that total distance of transect lines covered, 19,996 km was surveyed on the 6 southern CalCOFI lines (hereafter referred to as "the study area") in acceptable weather conditions (sea state of 0–5). Within the study area, on-effort transect line kilometers surveyed did not vary significantly by season (ANOVA, F=0.078, P=0.97). Sea states varied by season, with greatest sea states during spring and summer and lowest sea states during winter (Kruskal-Wallis one-way ANOVA, P<0.001). The median sea state was 3 in all seasons, except for summer, when it was 4. We found no significant difference in perpendicular distance to transect line for any species group by vessel (large whales, ANOVA, F=2.08, P=0.16; delphinids and porpoises ANOVA, F=1.01, P=0.39) or by vessel-season (large whales, ANOVA, F=2.76, P=0.15; delphinids and porpoises ANOVA, F=0.36, P=0.56).

As stated in the *Materials and methods* section, acceptable survey conditions required ≥0.9 km of estimated visibility on the transect line. Only 0.67% of effort was conducted with a visibility of ≤900 m, and that effort resulted in 4 sightings of common dolphins; because those dolphins were not identified to species level, their sightings were not used in the detection function. All encounters used in detection functions for the 3 species groups were made with at least 2.77 km visibility, with 93% of large whales, 94% of delphinids, and 100% of Dall's porpoises encountered with visibility ≥7.4 km.

In the study area during the 16 survey cruises, 29 marine mammal species were encountered, including 22 cetaceans, 6 pinnipeds, and a single mustelid species (Table 3). There were 931 on-effort sightings in the study area, with California sea lions (154 recorded sightings) the most commonly encountered species, followed by short-beaked common dolphins (122 sightings), northern fur seals (*Callorhinus ursinus*, 59 sightings), and fin whales (53 sightings). The most commonly encountered large cetaceans in the study area were fin, humpback (34 sightings), blue (25 sightings), and sperm (20 sightings) whales (Fig. 3), and the most commonly encountered small cetacean species were short-beaked common dolphin, Pacific white-sided dolphin (46 sightings), and Dall's porpoise (49 sightings) (Fig. 4). The ratio of on-effort sightings to opportunistic and off-effort sightings of cetaceans (1:0.76) in this study is higher than would be expected for other line-transect surveys where very little sighting effort is conducted off transect or in poor sea conditions. The large number of off-effort and opportunistic sightings in our study is mostly due to the large amount of opportunistic effort between the primary transect lines or at the water sampling stations along the coast.

Multispecies sightings were observed on 15 occasions for 7 dolphin species; the northern right whale dolphin and Pacific white-sided dolphin mixed most frequently (5 times), bottlenose dolphin and common dolphins mixed 3 times, Pacific white-sided dolphin and short-beaked common dolphin mixed 2 times, striped dolphin (*Stenella coeruleoalba*) and unidentified common dolphins mixed 2 times, and single occurrences

Table 3

Sighting data (number of encounters and estimated number of individuals) from 16 line-transect surveys conducted off Southern California from July 2004 to April 2008 on the 6 southern transect lines of quarterly California Cooperative Oceanic Fisheries Investigation (CalCOFI) cruises. Opportunistic effort is the category for sightings made off effort or when a vessel was not on a CalCOFI transect line.

	On effort		Opportunistic effort		Total	
Species	Number of encounters	Number of individuals	Number of enccounters	Number of individuals	Number of encounters	Number of individuals
Humpback whale	34	60	6	13	40	73
Blue whale	25	34	20	27	45	61
Fin whale	53	100	9	10	62	110
Minke whale	10	10	8	9	18	19
Sei whale	0	0	1	1	1	1
Bryde's/sei whale	1	1	1	1	2	2
Gray whale	8	16	16	33	24	49
Sperm whale	20	36	11	18	31	54
Baird's beaked whale	1	20	0	0	1	20
Cuvier's beaked whale	3	3	1	3	4	6
Killer whale	2	9	0	0	2	9
Short-finned pilot whale	1	33	1	30	2	63
False killer whale	1	10	0	0	1	10
Short-beaked common dolphin	122	11,067	96	8677	218	19,744
Long-beaked common dolphin	17	3259	39	7652	56	10,911
Common dolphin (unknown Short- or long-beaked)	72	6532	75	12,443	147	18,975
Pacific white-sided dolphin	46	573	34	467	80	1040
Risso's dolphin	14	205	25	505	39	710
Bottlenose dolphin	12	220	18	221	30	441
Northern right whale dolphin	13	480	12	245	25	725
Rough-toothed dolphin	0	0	1	9	1	9
Striped dolphin	2	77	1	7	3	84
Harbor porpoise	0	0	1	2	1	2
Dall's porpoise	49	267	24	115	73	382
Unidentified large cetacean	123	153	74	98	197	251
Unidentified small cetacean	63	5496	61	3703	124	9199
Unidentified *Mesoplodon*	1	1	0	0	1	1
Total for cetaceans	693	28,662	535	34,289	1228	62,951
California sea lion	154	1318	85	606	239	1924
Northern fur seal	59	78	14	20	73	98
Guadalupe fur seal	0	0	2	2	2	2
Steller sea lion	1	1	0	0	1	1
Northern elephant seal	11	11	2	2	13	13
Harbor seal	0	0	3	3	3	3
Sea otter	0	0	1	1	1	1
Unidentified fur seal	1	1	0	0	1	1
Unidentified pinniped	12	19	4	4	16	23
Total for pinnipeds or mustelids	238	1428	111	638	349	2066
Grand total	931	30,090	646	34,927	1577	65,017
Total transect line surveyed (km)	19,996		5083		25,079	

were recorded of Pacific white-sided dolphin with unidentified common dolphins, Risso's dolphin with northern right whale dolphin, and Risso's dolphin with bottlenose dolphin.

Harbor porpoise (*Phocoena phocoena*) were encountered on a single survey north of Point Conception and were excluded from analyses because the study area included only the very southern tip of the regular habitat of this species off California (Barlow, 1988; Forney et al., 1991). Rough-toothed dolphins (*Steno bredanensis*) and false killer whales (*Pseudorca crassidens*) were also encountered once each; both encounters were excluded

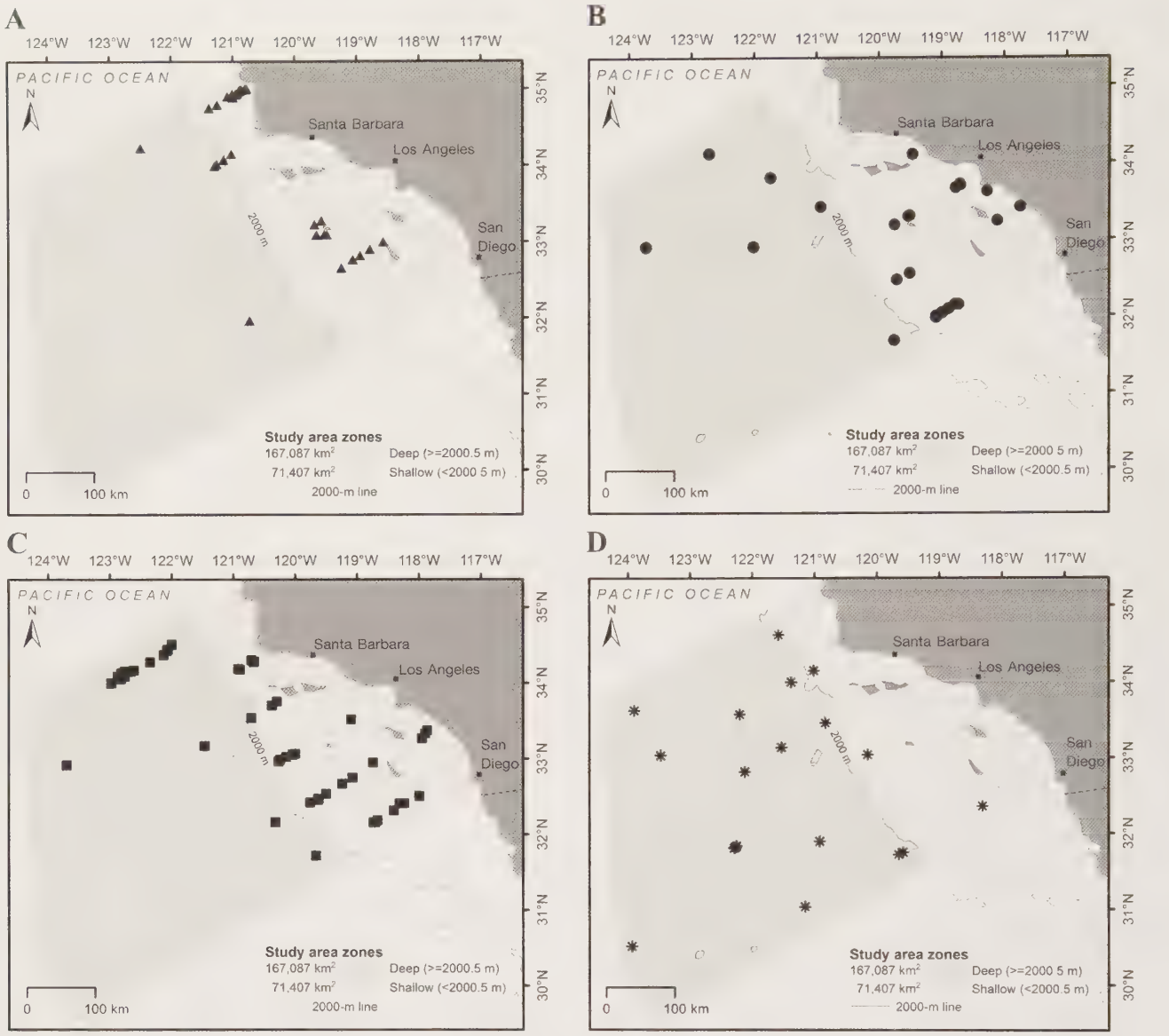

Figure 3

Maps of on-effort sightings of the 4 most commonly encountered species of large whales, the (**A**) humpback whale (*Megaptera novaeangliae*), (**B**) blue whale (*Balaenoptera musculus*), (**C**) fin whale (*B. physalus*), and (**D**) sperm whale (*Physeter macrocephalus*), recorded during the 16 shipboard line-transect surveys conducted quarterly during 2004–08 as part of the California Cooperative Oceanic Fisheries Investigation.

from analyses because the encounter records likely represent extralimital occurrences for both species.

Abundance estimates from line-transect data

Significant covariates for estimation of detection functions varied by species and species group (Table 2). On the basis of AIC values and visual examinations of test models, we selected sea state as a significant covariate for both the delphinid and Dall's porpoise group. Additionally, group size and dolphin species were chosen for the delphinid detection model. Average effective strip width (ESW) was 1294 m for large whales, 298 m for delphinids, and 305 m for porpoises.

Baleen whales We encountered 6 or possibly 7 species of baleen whales (one encounter was undetermined; it was not possible to distinguish whether it was a Bryde's or sei whale [*Balaenoptera edeni brydei*, *B. e. edeni*, or *B. borealis*]), and sample sizes by species were sufficient to calculate seasonal abundance and density estimates for 3 of those species. Fin whales had the

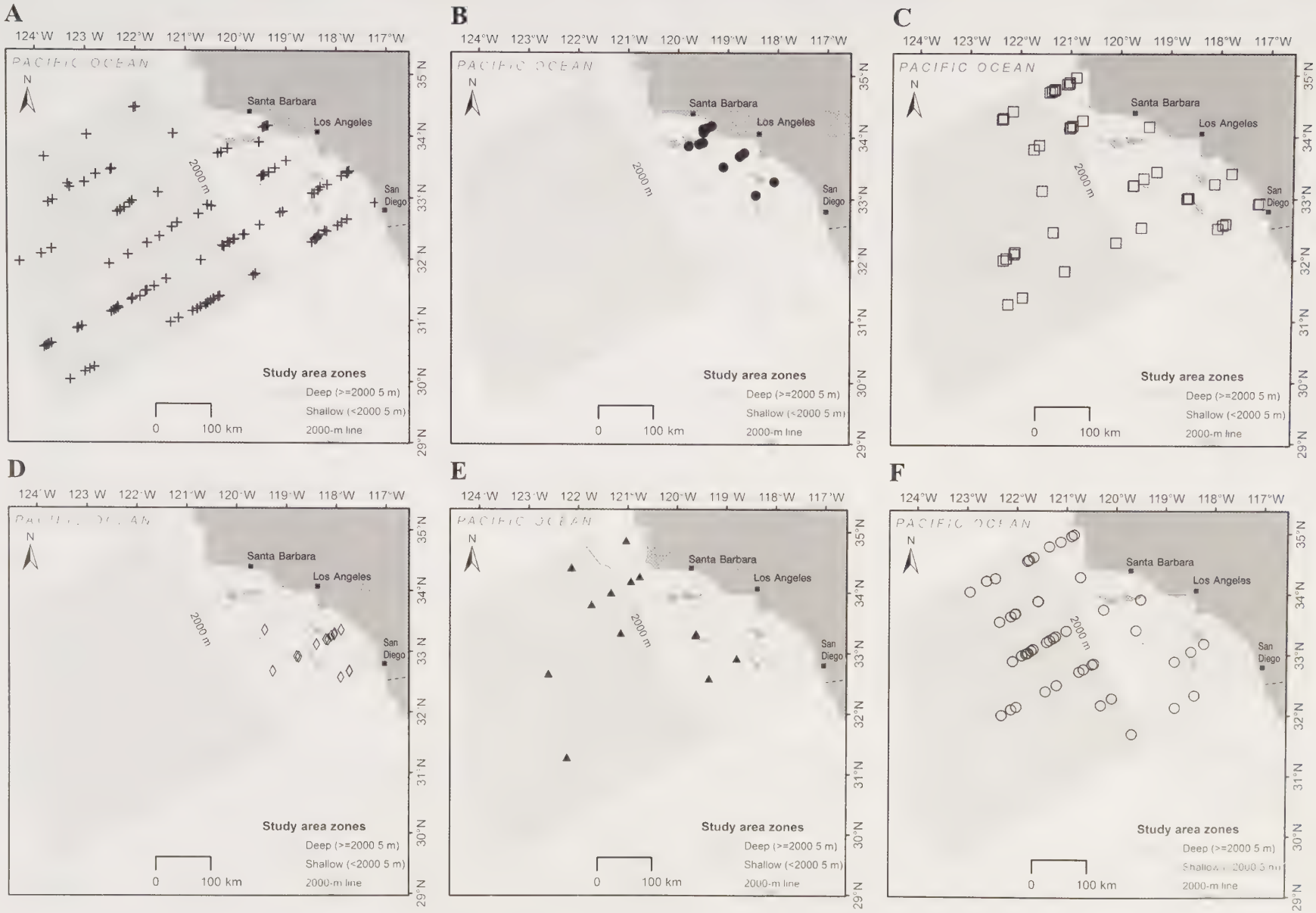

Figure 4

Map of on-effort sightings of the 5 most commonly encountered dolphin species, the (**A**) short-beaked common dolphin (*Delphinus delphis*), (**B**) long-beaked common dolphin (*D. capensis*), (**C**) Pacific white-sided dolphin (*Lagenorhynchus obliquidens*), (**D**) Risso's dolphin (*Grampus griseus*), and (**E**) northern right whale dolphin (*Lissodelphis borealis*), and of the (**F**) Dall's porpoise (*Phocoenoides dalli*) recorded during the 16 shipboard line-transect surveys conducted quarterly during 2004–08 as part of the California Cooperative Oceanic Fisheries Investigation.

Table 4

Encounter rate, the number of encounters (Enc) per 1000 km, and number of sightings *n* of cetacean species by season on the 6 southern transect lines during 16 quarterly California Cooperative Oceanic Fisheries Investigation (CalCOFI) cruises conducted from 2004 to 2008 off Southern California, for species seen on 10 or more occasions. The value under each season represents the combined length of the transect lines surveyed.

Species	Winter (4165 km) Enc/1000 km, *n*	Spring (4904 km) Enc/1000 km, *n*	Summer (6211 km) Enc/1000 km, *n*	Fall (4716 km) Enc/1000 km, *n*	All seasons (19,996 km) Enc/1000 km, *n*
Humpback whale	0, 0	2.2, 11	1.6, 10	2,7, 13	1.7, 34
Blue whale	0, 0	0, 0	3.1, 19	1.3, 6	1.3, 25
Fin whale	0.7, 3	1.0, 5	3.7, 23	4.7, 22	2.7, 53
Minke whale	0, 0	1.4, 7	0.3, 2	0.2, 1	0.5, 10
Sperm whale	1.0, 4	0.4, 2	1.9, 12	0.4, 2	1.0, 20
Short-beaked common dolphin	7.2, 30	0.8, 4	9.5, 59	6.1, 29	6.1, 122
Long-beaked common dolphin	0.2, 1	0.2, 1	1.3, 8	1.5, 7	0.9, 17
Common dolphin (unknown short- or long-beaked)	2.6, 11	1.6, 8	5.5, 34	4.0, 19	3.6, 72
Pacific white-sided dolphin	2.6, 11	4.7, 23	1.1, 7	1.1, 5	2.3, 46
Risso's dolphin	0.7, 3	1.6, 8	0.2, 1	0.4, 2	0.7, 14
Bottlenose dolphin	0.5, 2	1.0, 5	0.2, 1	0.8, 4	0.6, 12
Northern right whale dolphin	0.2, 1	1.8, 9	0, 0	0,6, 3	0.7, 13
Dall's porpoise	2.6, 11	7.1, 35	0.2, 1	0.4, 2	2.5, 49

highest encounter rate (Table 4) and were the most abundant of large whales in the study area (Table 5), with the greatest density estimate from summer–fall surveys in shallow water, 3.67 individuals/1000 km^2 (CV=0.30) (Tables 6 and 7), and with the greatest abundance during the summer–fall surveys in deep water. Fin whales were the only whale species that showed a significant difference in depth, distance to land, and distance to shelf by seasonal period (Table 7; Figs. 5 and 6). Humpback whale density was highest during the summer–fall surveys in shallow water with 3.08 individuals/1000 km^2 (CV=0.36) (Table 5). Least abundant of the large whales, blue whales were encountered only during the summer–fall surveys, with the greatest density and abundance in shallow water, 3.20 individuals/1000 km^2 and 228 individuals (CV=0.26) (Table 5).

Odontocetes Although sperm whales were most abundant during the summer–fall surveys in deep water, 158 individuals (CV=0.36) (Table 5), density was similar for both shallow areas (0.94 individuals/1000 km^2 [CV=0.44]) and deep areas (0.95 individuals/1000 km^2 [CV=0.36]) for that seasonal period. Short-beaked common dolphins were the most abundant cetacean species, encountered in all seasons and at all depths; the highest encounter rate was observed in the summer months (Table 4) and the greatest density estimate was obtained from summer–fall surveys in shallow water, 1319.69 individuals/1000 km^2 (CV=0.24) (Table 5). Long-beaked common dolphins were the second-most abundant cetacean species; however, this species was encountered only in shallow water and, seasonally, there was a dramatic shift in density with 22 times more long-beaked common dolphins observed during the summer–fall surveys than during the winter–spring surveys (Table 5). Because of the difficulty of distinguishing between short- and long-beaked common dolphins from a survey conducted in passing mode, 72 out of 211 on-effort common dolphin sightings were not identified to species (Table 3). Densities of Pacific white-sided, northern right whale, and Risso's dolphins were greatest during the winter–spring period in shallow water, and Dall's porpoises were most abundant during the winter–spring seasonal period in deep water; these species were least abundant during the summer–fall period. Abundance of Dall's porpoises varied strongly by seasonal period but not by depth. Beaked whales were encountered on 6 occasions, with Cuvier's beaked whale (*Ziphius cavirostris*) the most commonly encountered (3 occasions).

Discussion

Monitoring and management of marine mammal species off Southern California has often relied heavily on abundance estimates generated from line-transect surveys conducted during the summer and fall, despite year-round anthropogenic activities and significant seasonal spatial movements of many species (Forney and Barlow, 1998). Our observations from the 16 CalCOFI surveys conducted between 2004 and 2008 provide the most current and consistent data set on seasonal shifts in movements and abundance for the most commonly

Table 5

Density and abundance of cetaceans by species and season-and-depth stratum. The total area of the study area was 238,494 km^2, with 71,407 km^2 in shallow depths (<2000.5 m) and 167,087 km^2 in deep depths (≥2000.5 m). Coefficients of variation (CV) apply to both density and abundance estimates, and "NA" indicates that no CV was available because of a sample size equal to zero. Asterisks indicate mean values derived from the separate stratified densities for shallow and deep waters. See Table 2 for covariates used to estimate density by species group.

Species Season, depth	Number of groups	Mean group size	Density (individuals/ 1000 km^2)	Uncorrected abundance	CV
Blue whale					
Winter–spring, shallow	0	0.0	0.00	0	NA
Winter–spring, deep	0	0.0	0.00	0	NA
Summer–fall, shallow	19	1.4	3.20	228	0.26
Summer–fall, deep	5	1.2	0.36	59	0.33
Summer–fall, all depths	24	1.4	1.21*	288	0.23
Fin whale					
Winter–spring, shallow	7	2.0	2.33	166	0.30
Winter–spring, deep	0	0.0	0.00	0	NA
Summer–fall, shallow	22	1.4	3.67	262	0.30
Summer–fall, deep	21	2.0	2.49	417	0.42
Summer–fall, all depths	43	1.6	2.84*	679	0.25
Humpback whale					
Winter–spring, shallow	8	2	2.66	190	0.33
Winter–spring, deep	3	1.7	0.34	56	0.58
Winter–spring, all depths	11	1.9	1.03*	246	0.29
Summer–fall, shallow	19	1.4	3.08	220	0.36
Summer–fall, deep	2	4.5	0.53	89	0.58
Summer–fall, all depths	21	1.7	1.29*	309	0.32
Sperm whale					
Winter–spring, shallow	1	5	0.83	59	0.70
Winter–spring, deep	5	1.2	0.40	67	0.40
Summer–fall, shallow	3	2.7	0.94	67	0.44
Summer–fall, deep	10	1.6	0.95	158	0.36
Short-beaked common dolphin					
Winter–spring, shallow	11	57.6	307.83	21,981	0.33
Winter–spring, deep	22	127.8	609.86	101, 900	0.45
Winter–spring, all depths	33	104.3	519.43*	123,881	0.21
Summer–fall, shallow	33	104.8	1319.69	94,235	0.24
Summer–fall, deep	51	37.5	454.35	75,916	0.20
Summer–fall, all depths	84	63.9	713.44*	170,151	0.14
Long-beaked common dolphin					
Winter–spring, shallow	1	60	30.90	2207	0.78
Winter–spring, deep	0	0.0	0.00	0	NA
Summer–fall, shallow	14	217.2	687.87	49,118	0.52
Summer–fall, deep	0	0.0	0.00	0	NA
Pacific white-sided dolphin					
Winter–spring, shallow	19	13.2	110.57	7896	0.38
Winter–spring, deep	14	14	41.91	7002	0.35
Winter–spring, all depths	33	13.5	62.46*	14,898	0.21
Summer–fall, shallow	11	6.6	29.24	2088	0.34
Summer–fall, deep	1	3	0.6967	116	0.72
Summer–fall, all depths	12	6.3	9.24*	2204	0.35
Risso's dolphin					
Winter–spring, shallow	9	19	35.65	2546	0.36
Winter–spring, deep	0	0.0	0.00	0	NA
Summer–fall, shallow	3	8.6	3.90	279	0.55
Summer–fall, deep	0	0.0	0.00	0	NA

table continued

Table 5 (continued)

Species Season, depth	Number of groups	Mean group size	Density (individuals/ 1000 km$^{2)}$	Uncorrected abundance	CV
Bottlenose dolphin					
Winter–spring, shallow	4	11.2	22.12	1580	0.54
Winter–spring, deep	1	2	0.97	161	0.79
Summer–fall, shallow	5	13.6	40.32	2879	0.69
Summer–fall, deep	0	0.0	0.00	0	NA
Northern right whale dolphin					
Winter–spring, shallow	5	39	107.31	7662	0.50
Winter–spring, deep	4	13.5	20.30	3392	0.49
Summer–fall, shallow	1	6	6.72	480	0.78
Summer–fall, deep	2	25	11.10	1855	0.68
Dall's porpoise					
Winter–spring, shallow	13	4.8	45.50	3249	0.32
Winter–spring, deep	32	5.3	48.65	8128	0.28
Winter–spring, all depths	45	5.1	47.71*	11,378	0.26
Summer–fall, shallow	2	3	2.11	151	0.58
Summer–fall, deep	1	17	2.73	456	0.78

encountered marine mammal species in the Southern California region. Although seasonal variation was seen in cetacean encounters, large numbers of whales and dolphins were observed year-round off Southern California, both on and between transect lines (Table 4; Figs. 3 and 4).

Abundance and density of cetaceans: overall comparisons with previous surveys

Although our analyses of relative density by seasonal period and depth are robust for the most commonly encountered species, absolute densities and uncorrected abundances reported here may differ from values reported by the NOAA Southwest Fisheries Science Center (SWFSC) for its previous studies in Southern California; those differences primarily are due to 5 factors. First, our study relied on data collected by the naked eye or with 7× binoculars, hence ESWs by species group in our study were calculated as half (or less) of the ESWs used for the same species groups from 5 years of pooled SWFSC sighting data, which were collected with 25× binoculars as the primary search method (Barlow and Forney, 2007). Second, we assumed that detection on the transect line was certain, or $g(0)=1$; this decision likely had the greatest negative impact on density of cryptic or long-diving species, like sperm whales. Third, we had a relatively high proportion of sightings that were not identified to species, and we did not prorate unidentified cetaceans, thinking that it would be better to compute a best estimate of cetaceans positively identified to species than to make assumptions about the detectability of unidentified and identified species. Fourth, we used uncalibrated group-size estimates—an approach different from the one for SWFSC cruises in which observers make group-size estimates independently and each observer is "calibrated" with the use of photogrammetry of select sightings (Gerrodette and Perrin[4]). Carretta et al. (2011b) stated that uncalibrated group-size estimates could result in estimated counts that were 50% lower than actual group sizes. Fifth, we did not correct for reactions to vessel approach by small cetaceans—an issue that is primarily a concern with the Dall's porpoise and vessel-attracted dolphin species, like the short-beaked common dolphin. Lastly, the SWFSC southern stratum, with an area of 318,500 km^2, is larger than the study area of the CalCOFI surveys by 25%. We compared density and abundance of species from these 2 studies because the 2 areas overlap by 75% and the CalCOFI study area occurs completely inside the SWFSC southern stratum. That said, our study provides the most recent and best replicated shipboard assessment of seasonal densities for 11 species of cetaceans off Southern California, including 3 species of baleen whales, the sperm whale, 6 species of delphinids, and the Dall's porpoise.

Baleen whales The most commonly occurring large whales that used this area for feeding were fin, humpback, and blue whales; because of their presence along the coast in greater numbers during the summer and fall, compared with other seasons, these species have been well represented in previous line-transect and

[4] Gerrodette, T., and C. Perrin. 1991. Calibration of shipboard estimates of dolphin school size from aerial photographs. Southwest Fish. Sci. Cent. Admin. Rep. W-91-36, 73 p.

Table 6

Analysis of seasonal habitat use by cetacean species encountered on the 6 southern transect lines of 16 California Cooperative Oceanic Fisheries Investigation (CalCOFI) cruises conducted from 2004 to 2008 off Southern California. Values of mean depth, mean distance from land (Mean Dist Land), and mean distance to the mainland (Mean Dist Mainland) are for all cetacean species for which there were 10 or more on-effort encounters on the 6 CalCOFI transect lines; an exception was made for striped dolphins, where $n=2$. For sample sizes, see Table 4. Standard deviations (SD) of mean depths and mean distances from land are shown in parentheses. SDs were not available (NA) if only a single sighting was made during a season. The value under each season represents the combined length of the transect lines surveyed.

	Winter (4165 km)			Spring (4904 km)			Summer (6211 km)			Fall (4716 km)			All Seasons (19,996 km)		
Species	Mean Depth (SD)(m)	Mean Dist Land (km)	Mean Dist Mainland (km)	Mean Depth (SD)(m)	Mean Dist Land (km)	Mean Dist Mainland (km)	Mean Depth (SD)(m)	Mean Dist Land (km)	Mean Dist Mainland (km)	Mean Depth (SD)(m)	Mean Dist Land (km)	Mean Dist Mainland (km)	Mean Depth (SD)(m)	Mean Dist Land (km)	Mean Dist Mainland (km)
Whales															
Humpback	–	–	–	1395 (1369)	50 (47)	87	179 (127)	18 (16)	18	911 (1140)	36 (44)	78	852 (1132)	35 (40)	63
Blue	–	–	–	–	–	1551 (1342)	82 (78)	130	1710 (1708)	72 (66)	127	1589 (1401)	79 (74)	129	
Fin	761 (620)	26 (18)	88	965 (530)	45 (31)	66	1790 (1434)	82 (70)	133	3105 (1529)	144 (67)	170	2200 (1593)	102 (74)	139
Minke	–	–	–	708 (353)	34 (12)	53	250 (80)	7 (4)	55	53 (NA)	2 (NA)	2	551 (388)	25 (17)	48
Sperm	3729 (353)	236 (173)	304	2460 (1889)	116 (103)	194	3367 (1172)	199 (103)	227	2587 (2353)	174 (166)	223	3270 (1209)	195 (118)	238
Delphinids															
Short-beaked common	2942 (1613)	258 (186)	315	2470 (1955)	297 (204)	373	2517 (1579)	127 (101)	184	2807 (1624)	172 (115)	219	2689 (1600)	176 (143)	231
Long-beaked common	51 (NA)	12 (NA)	12	1232 (NA)	11 (NA)	68	215 (227)	9 (6)	96	453 (427)	18 (8)	18	363 (398)	12 (7)	29
Pacific white-sided	1836 (1859)	87 (104)	134	2126 (1772)	113 (98)	133	1430 (937)	66 (28)	81	291 (288)	12 (5)	54	1751 (1660)	89 (90)	117
Risso's	663 (230)	31 (21)	81	902 (387)	29 (15)	64	795 (NA)	19 (NA)	34	920 (151)	11 (3)	46	846 (318)	26 (15)	63
Bottlenose	949 (448)	11 (3)	83	1015 (1602)	74 (128)	128	260 (NA)	4 (NA)	54	400 (210)	5 (1)	24	736 (1034)	34 (84)	80
Northern right whale	640 (NA)	64 (NA)	153	2023 (1770)	98 (112)	138	–	–	–	2666 (1581)	86 (46)	86	2065 (1663)	92 (94)	128
Striped	–	–	–	–	–	–	4075 (54)	294 (159)	326	–	–	–	4075 (54)	294 (159)	326
Porpoise															
Dall's porpoise	2700 (1598)	108 (68)	141	2933 (1444)	120 (68)	158	1135 (NA)	93 (NA)	93	2134 (2718)	92 (125)	107	2811 (1501)	115 (68)	151

Table 7

Summary of results from Kruskal-Wallis and Mann-Whitney tests of seasonality for depth, distance from vessel to land, and distance from vessel to shelf break for cetaceans encountered on the transect lines of the California Cooperative Oceanic Fisheries Investigation (CalCOFI) surveys conducted from 2004 to 2008 across all 4 seasons. Probability values that indicate significant results are shown in bold type. Asterisks indicate species for which tests were run with a limited number of sightings for one or more seasons; see Table 4 for number of sightings.

Species	Depth (*P*-value)	Distance to land (*P*-value)	Distance to shelf break (*P*-value)
Humpback whale	**0.007**	0.149	0.191
Blue whale	0.799	0.611	0.484
Fin whale*	**0.003**	**<0.000**	**0.001**
Minke whale	0.079	0.040	0.143
Sperm whale*	0.783	0.729	0.732
Short-beaked common dolphin*	0.122	**0.005**	**0.008**
Long-beaked common dolphin	0.247	0.037	0.015
Common dolphin (unknown short- or long-beaked)	0.773	0.422	0.587
Pacific white-sided dolphin	**0.014**	**0.005**	**0.008**
Risso's dolphin*	0.581	0.136	0.087
Bottlenose dolphin*	0.256	0.223	0.252
Northern right whale dolphin*	0.518	0.518	0.518
Dall's porpoise*	0.889	0.941	0.929

photoidentification studies. The large whales represented here are highly visible from a distance and often occur in small groups; therefore, confidence levels on group-size estimates are higher and abundance estimates likely are more accurate for them than for the smaller cetaceans that occur in large and more variable size groups. Group sizes for fin, humpback, and blue whales (Table 5) were similar to group sizes reported by Barlow (2010) and Barlow and Forney (2007). The number of unidentified large cetacean encounters (123) is to be expected from a survey conducted in passing mode. Although we did not apportion encounters of unidentified species in our analyses, on the basis of the proportion of large whale species positively identified, it is likely that fin, humpback, and blue whales made up the majority of these sightings.

Fin whales were the most commonly encountered and most abundant large whale in the study area. As has been documented by Forney and Barlow (1998), fin whales were encountered during all seasons, but the encounter rate for this species increased during the summer and fall seasons. Our abundance of 679 individuals (CV=0.25) in the study area during the summer–fall seasonal period is similar to Barlow's (2010) estimate of 499 individuals (CV=0.27) from a 2008 survey for Southern California and higher than the abundance estimate of 359 individuals (CV=0.40) from surveys conducted in 1991–2005 (Barlow and Forney, 2007). Given the differences in survey design, we would have expected our abundance estimate to have been lower than the values presented in Barlow (2010); however, annual variability, which we do not address in this study of multiyear CalCOFI surveys, may account for the difference in abundance estimates. Broadly, these patterns of increasing abundance are consistent with the recently documented trend of an increasing population for fin whales (Moore and Barlow, 2011). Although there were few encounters during winter, fin whales used nearshore waters in the winter and spring and shifted into offshore waters in the summer and fall (Tables 6 and 7; Figs. 5 and 6); this movement seems to coincide with the observed coldest temperatures in nearshore waters recorded in winter and spring and with a slight increase of zooplankton biomass that occurs in the spring (Munger et al., 2009).

Although humpback whales were the second-most frequently encountered large cetacean, none were sighted during the winter. Our abundance estimate of 309 individuals (CV=0.32) for the summer–fall period is almost 6 times larger than the estimates of 49 individuals (CV=0.43) from the 2008 survey (Barlow, 2010) and of 36 whales (CV=0.51) from pooled 1991–2005 surveys (Barlow and Forney, 2007); however, just over half of our on-effort humpback sightings came from the 2007 summer cruise near Point Conception, where and when zooplankton abundance was notably high (Munger et al., 2009), indicating that an unusually large proportion of the population shifted into this area to take advantage of available prey. Because Southern California represents the southern end of the humpback whale's feeding range, such annual variation in available prey could strongly affect the abundance of

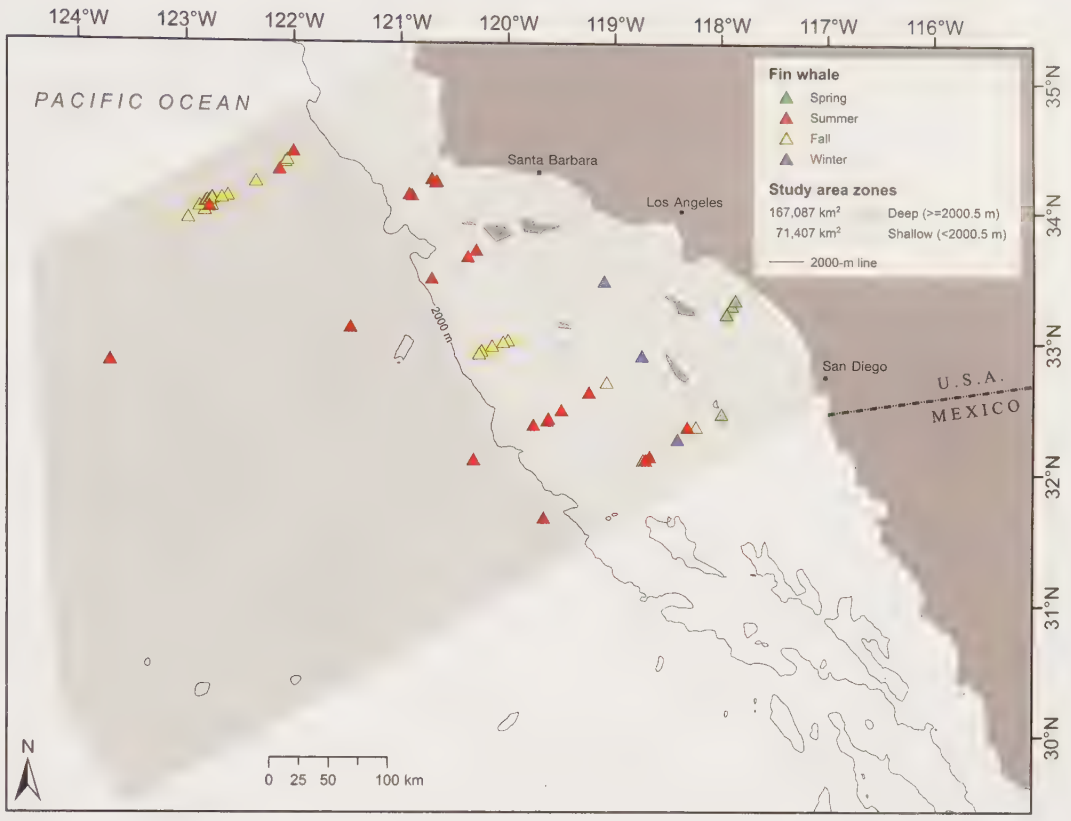

Figure 5

Map of on-effort encounters with the fin whale (*Balaenoptera physalus*) by season, recorded during the 16 shipboard line-transect surveys conducted quarterly during 2004–08 as part of the California Cooperative Oceanic Fisheries Investigation. The color of the triangle indicates the season: blue=winter, green=spring, red=summer, and yellow=fall.

this species in our study area. Humpback whales off California, Oregon, and Washington migrate seasonally to wintering grounds off Baja, California, mainland Mexico, and Central America (Steiger et al., 1991; Calambokidis et al., 2000; Urbán et al., 2000). Clapham et al. (1997) and Forney and Barlow (1998) noted that in waters off California, a significantly greater proportion of the humpback whale population was found farther offshore in winter than in summer. We also found that more humpback whales occurred farther offshore and in deeper water in spring than during the summer–fall seasonal period (Table 6).

The thirdmost frequently encountered and abundant baleen whale within the study area, the blue whale, showed a distinct seasonal presence, a result that concurs with the findings from year-round aerial and ship-based surveys off Southern California. Forney and Barlow (1998) and Larkman and Veit (1998) found the greatest abundance of blue whales during August–October. Our abundance estimate of 288 blue whales (CV=0.23) was much lower than Barlow and Forney's (2007) estimate of 842 individuals (CV=0.20) off Southern California. The discrepancy between these estimates is likely due to a few factors, including interannual differences in proportion of the population found within the study area and our lack of a correction factor for transect-line detection probability. Barlow and Forney's (2007) estimate included surveys completed in 1991, 1993, and 1996, all years when much of the blue whale population was thought to be feeding along the California coast; however, in more recent years, evidence has indicated that blue whales are using more northerly, southerly, and offshore waters (Calambokidis and Barlow, 2004; Barlow and Forney, 2007; Calambokidis et al., 2009). No blue whales were encountered in the study area during the winter–spring period—a finding that corresponds to their known migration pattern of feeding off California from May to November and migrating south to spend winter and spring off Mexico (Calambokidis et al., 1990; Mate el al., 1999; Stafford et al., 1999) and as far south as 6°N at the Costa Rica Dome (Wyrtki, 1964).

Although known to be present year-round (Dohl et al.[5]; Forney et al., 1995; Barlow[3]), minke whales

[5] Dohl, T. P., R. C. Guess, M. L. Duman, and R. C. Helm. 1983. Cetaceans of central and northern California, 1980–1983: status, abundance, and distribution. Part of investigator's fi-

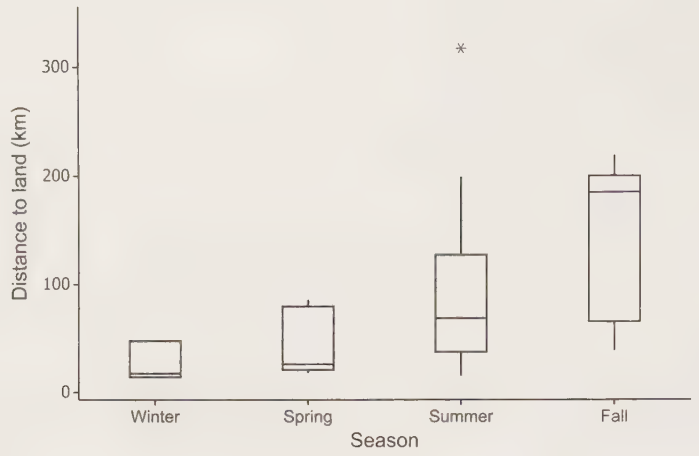

Figure 6

Box-and-whisker plot showing distance to land by season for fin whales (*Balaenoptera physalus)* within the study area for line-transect surveys conducted off Southern California during 2004–08 for 16 quarterly California Cooperative Oceanic Fisheries Investigation cruises. In each box, the middle horizontal line shows the median value and the upper and lower lines show the 75th and 25th percentiles. Ends of the upper and lower whiskers indicate the minimum and maximum data values; an * indicates the outlier and the vertical lines extend to a maximum of 1.5 times the interquartile range.

(*Balaenoptera acutorostrata*) are difficult to sight even in very good sea conditions. The sample size of this species in the 6 CalCOFI surveys was insufficient for an abundance estimate, but it is worth noting that we encountered minke whales in low numbers from spring to fall, and a peak in encounter rates occurred during the spring (Table 4) that cannot be explained by better sea conditions in spring. Although sei whales were historically the fourth-most commonly captured whale along coastal California during whaling activity in the 1950s and 1960s (Rice, 1974), they now are considered rare in California waters (Dohl et al.[5]; Mangels and Gerrodette, 1994; Forney et al., 1995; Barlow[3]). Our results support findings that they are not commonly encountered off southern California with only a single sighting of a sei whale and a sighting of one other individual that was either a sei whale or a Bryde's whale.

Odontocetes We encountered 16 species of odontocetes, with sufficient sightings of 8 species to calculate seasonal abundance and density and examine seasonal trends. The most commonly encountered odontocete species along Southern California are present year-round, although some of them undergo seasonal shifts in abundance; the Dall's porpoise and Risso's dolphin have been recognized as moving seasonally into Southern California waters during the winter months. Such seasonal shifts of abundance out of Southern California waters during winter months increases the likelihood that these species were regionally underrepresented in previous estimates (Barlow and Forney, 2007; Carretta et al., 2011b) of density and abundance that were generated from sighting data collected during summer–fall ship-based surveys.

Sufficient sample size allowed for density and abundance estimation of sperm whales; however, mean group size (2.7 individuals) was significantly lower than the 8.1 individuals reported off Southern California from pooled sightings collected over 5 years of SWFSC surveys (Barlow and Forney, 2007). In our study, group-size estimates were very likely negatively biased by the constraints of conducting a survey in passing mode, instead of using the protocol for the SWFSC line-transect surveys of conducting multiple counts over 90 min to enumerate asynchronously diving whales (Barlow and Taylor, 2005; Barlow and Forney, 2007). We encountered sperm whales year-round and in both depth categories, but we observed this species primarily during the summer–fall period in depths >2000.5 m—findings similar to earlier analyses of year-round survey effort (Dohl et al.[5]; Barlow, 1995; Forney et al., 1995).

Even with our relatively high number of common dolphin sightings that could not be identified to species, we found that short-beaked common dolphins were the most abundant and widely distributed cetacean in our study area—a finding that is consistent with previously published results from cetacean survey effort off Southern California (Leatherwood et al., 1982; Dohl et al., 1986; Smith et al., 1986; Barlow, 1995; Forney et al., 1995). Moreover, our stratified abundance estimates provide clear evidence of seasonal shifts in habitat use. We found that, during the summer–fall period, short-beaked common dolphins were fairly evenly spread throughout the study area, and, during the winter–spring period, there was a surge in abundance of this species into offshore waters (mean group size: 127.7 individuals; abundance: 101,900 individuals [CV=0.45]). The greatest seasonal abundance estimate (170,151 individuals [CV=0.14]) was from the summer–fall period, a level that is very close to Barlow and Forney's (2007) estimate for that seasonal period of 165,400 individuals (CV=0.19). From aerial and ship-based line-transect surveys, the abundance of short-beaked common dolphins off California has been shown to change on seasonal and interannual times scales (Dohl et al., 1986; Barlow, 1995; Forney et al., 1995).

nal report, Marine Mammal and Seabird Study, central and northern California, Contract No. 14-12-0001-29090. Prepared by Center for Marine Sciences, Univ. California, Santa Cruz, for the Pacific OCS Region, Minerals Management Service, OCS Study MMS 84-0045, 284 p.

Long-beaked common dolphins were the fourthmost commonly encountered and secondmost abundant small cetacean in the study area. Distribution of long-beaked common dolphins was limited to waters near the California coast or Channel Islands—a result that is consistent with findings that this species is commonly found within ~93 km of the coast and ranges from Baja California to central California, with the highest densities observed during warm-water events throughout their range (Heyning and Perrin, 1994). The uncorrected abundance estimate from summer–fall surveys at shallow depths for long-beaked common dolphins (49,118 individuals [CV=0.52]) was about 3 times higher than Barlow's (2010) abundance estimate determined from pooled data from line-transect surveys conducted during 1991–2008, but our mean group size (217.2 individuals [CV=0.52]) and abundance estimate were much lower than his mean group size and abundance estimates from the 2009 line-transect survey, where corrected mean group size was 481.0 individuals and abundance was 111,738 individuals (CV=0.44) (Carretta et al., 2011a). Our estimates are likely negatively biased, given the relatively large number of common dolphin sightings that were not identified to species. However, the 2009 estimates were much greater than the results from earlier surveys, and there was an indication that the moderate El Niño event in 2009 may have caused an influx of dolphins from the south. Our surveys, conducted during 2004–08, show that this species is present year-round but increases 22-fold in abundance during the summer–fall period, indicating that dolphins are shifting south for the winter and spring.

Although the number of sightings was insufficient from the winter–spring period to quantify year-round seasonality of long-beaked common dolphins, this study is the first to provide evidence of seasonal habitat use for the 2 common dolphin species found along Southern California. For previous publications that have documented seasonality, aerial surveys were used for cold-water seasonal surveys; however, at the time of those studies, there was not an effective method for distinguishing the 2 species from an aerial platform (Dohl et al., 1986; Forney et al., 1995; Forney and Barlow, 1998). In marked contrast to the ratio of encounters of short- and long-beaked common dolphins reported here (6:1), Carretta et al. (2011a) encountered the 2 species at a 1:1 ratio in 2009; their observation supports the hypothesis of a dramatic shift or pronounced interannual variability from the preceding years off Southern California.

Pacific white-sided dolphins were encountered in all seasons, with the greatest abundance estimate (14,898 individuals [CV=0.21]) from both depth categories combined in the winter–spring seasonal period. Although density was markedly different between the shallow and deep categories during the winter–spring season, abundance was fairly constant throughout the entire study area. During the summer–fall period, we found that density and abundance (9.24 individuals/1000 km^2; 2204 individuals [CV=0.35]) decreased by almost 15% from the previous winter–spring period, with greater abundance in shallow waters than in deep waters. Barlow and Forney (2007) published a similar pooled abundance estimate of 2196 individuals (CV=0.39) for surveys conducted in all depths during the summer–fall period during 1991–2005. From the data on encounters by season, we found that a significant shift into deep water occurred during the winter–spring period (Table 7, Fig. 7). Along the coast of California, the 2 forms of Pacific white-sided dolphins are primarily found in waters over the continental shelf and slope (Forney, 1994). The northern form is thought to enter coastal Southern California waters during the winter months and to congregate with the southern form (Walker et al., 1986; Lux et al., 1997; Soldevilla et al., 2011). Because we were unable to differentiate between the 2 forms, it is possible that the increase in observed abundance during the winter–spring season was a result of capturing both forms that use the study area rather than capturing only the southern form.

Risso's dolphins were encountered year-round in shallow water, with abundance estimates of 2546 individuals (CV=0.36) for the winter–spring period and of 279 individuals (CV=0.55) for the summer–fall period. Our findings agreed with those from visual surveys that found high seasonal variability in occurrence and distribution of this species off California (Shane, 1994; Forney and Barlow, 1998; Kruse et al., 1999; Benson et al., 2002; Barlow and Forney, 2007) and that their abundance along the California coast could be an order of magnitude higher during the winter than during the summer (Forney and Barlow, 1998). However, further research is needed to understand our results in relation to the findings of Soldevilla et al. (2010), who found peak Risso's dolphin echolocation activity off Southern California in the fall.

On the basis of genetics and morphology, bottlenose dolphins along the coast of California and elsewhere worldwide are split into offshore and coastal populations (Hansen, 1990; Carretta et al., 1998; Defran and Weller, 1999; Bearzi et al., 2009; Perrin et al., 2011). The Southern California coastal population typically is encountered within 500 m of shore (this species was sighted within that boundary 99% of the time during a previous study; Hanson and Defran [1993]), and the offshore population is found outside of a few kilometers from the mainland. The mean distance from a land mass that bottlenose dolphins were recorded in this study was 34 km; the minimum distance was just over 2 km. The study area did not include nearshore waters sufficiently to encounter coastal bottlenose; therefore, we assume that our abundance estimate is for the offshore bottlenose dolphin population. For our stratum of the summer–fall period and shallow depth, the abundance estimate (2879 individuals [CV=0.69]) is greater than Barlow and Forney's (2007) abundance estimate (1831 individuals [CV=0.47]) for this population off Southern California during the same period.

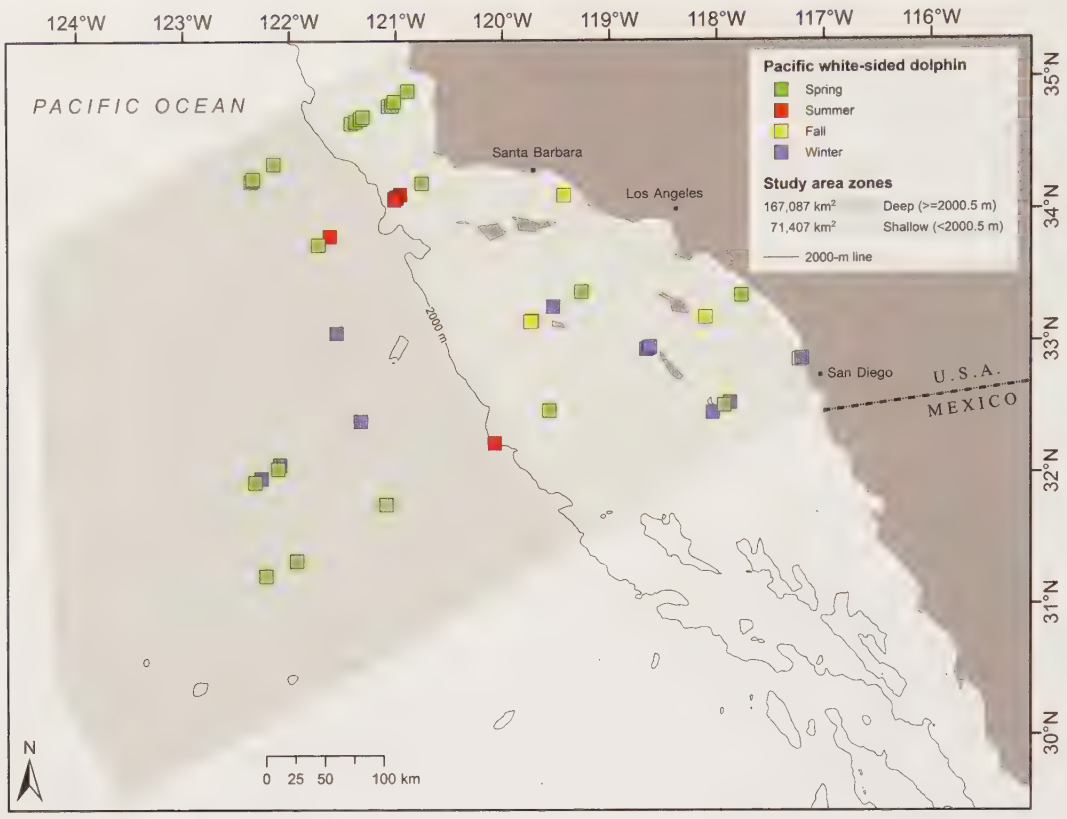

Figure 7

Map of on-effort encounters with the Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) by season during the 16 shipboard line-transect surveys conducted quarterly during 2004–08 as part of the California Cooperative Oceanic Fisheries Investigation. The color of the triangle indicates the season: blue=winter, green=spring, red=summer, and yellow=fall.

In addition to the high CV value associated with our abundance estimate, a likely cause of this discrepancy between the 2 studies is the difference in estimated group size, where we observed an average of 40.5 individuals in a group and Barlow and Forney (2007) reported 13.4 individuals in a group.

The Northern right whale dolphin and Dall's porpoise are known to favor cold waters, and we found both species to have the greatest abundance estimates during the winter–spring period over all depths. Although encounters with northern right whale dolphins in the summer–fall period were few, an increase in density during the winter–spring surveys in shallow water was observed—a finding that is consistent with earlier records that found this species beyond the continental slope for warm-water seasons and in shelf waters of the Southern California Bight for the cold-water season (Barlow, 1995; Forney et al., 1995; Forney and Barlow, 1998).

Although seasonally abundant, Dall's porpoises are often initially sighted when they react to survey vessels, thereby biasing abundance estimates upward. To compensate for vessel attraction, Barlow and Forney (2007) included only Dall's porpoise sightings made in sea states of 0–2—an approach that they noted limited sample size. On the basis of the detection model for Dall's porpoises (Fig. 2), which showed an even tapering of sightings with distance from the vessel, we included sightings in sea states of 0–5, assuming that it would be better to have a greater number of sightings than an insufficient number to estimate abundance. Spatially, our analysis of encounters with Dall's porpoises in the CalCOFI study area agrees with the finding of Morejohn (1979) that Dall's porpoises were commonly seen in small groups along the shelf and slope and in offshore waters. Dall's porpoises were consistently found in recently upwelled waters near shore (Peterson et al., 2006). In the CalCOFI study area, the highest encounter rates of Dall's porpoises occurred in spring, when upwelling waters were active.

As with the Dall's porpoise, many of the delphinids are known to react to a vessel before visual observers can detect them; this behavior is especially a concern when the naked eye and low-power binoculars are used in the search method, as they were in the CalCOFI surveys used in this study. Although reaction to vessel cannot be ruled out as a factor in our results, our decision to keep all on-effort sightings in the analyses was based on the detection model for delphinids (Fig.

3) that showed an even tapering of sightings with distance from vessel.

Our results on seasonal occurrence of the 6 frequently occurring delphinid species and the Dall's porpoise are consistent with prior findings. The bottlenose dolphin, long-beaked common dolphin, and short-beaked common dolphin generally favor warm-water (summer–fall) periods along the California coast (Dohl et al., 1986; Barlow, 1995; Forney et al., 1995). Dall's porpoise, the Pacific white-sided dolphin, the northern right whale dolphin, and Risso's dolphin commonly are found during the cold-water (winter–spring) periods off Southern California, and these species tend to migrate north into central California or Oregon and Washington during the warm-water periods (Forney, 1994; Forney and Barlow, 1998). These species have exhibited abundance shifts associated with oceanographic variability on both seasonal and interannual time scales (Perrin et al., 1985; Heyning and Perrin, 1994; Forney, 1997; Forney and Barlow, 1998; Becker, 2007).

There were only 6 sightings of beaked whales, but all 3 genera (*Ziphius*, *Berardius*, and *Mesoplodon*) known to be present off Southern California were detected. The single sighting of a *Mesoplodon* could not be confirmed to species. A single encounter with a group of Baird's beaked whales (*Berardius bairdii*) near the shelf break during a survey in the summer is consistent with other sightings of this species in continental slope waters from late spring to early fall (Balcomb, 1989; Carretta et al., 2011b).

Of the 11 dolphin species encountered, 5 species were represented by only 1–3 sightings per species: killer whale, false killer whale, short-finned pilot whale (*Globicephala macrorhynchus*), rough-toothed dolphin, and striped dolphin. Of these 5 species, only the killer whale is commonly found year-round off Southern California, with 2 U.S. stocks (Eastern North Pacific Transient and Eastern North Pacific Offshore [Carretta et al., 2011b]) that use the area. We were unable to confirm which stocks were represented in the 2 sightings of this species. The rough-toothed dolphin and false killer whale are considered rare off California, with no known current or historical populations along the West Coast of the United States; therefore, our sightings likely represent extralimital movements from populations farther south.

There were too few encounters with striped dolphins in the study area to look at seasonal shifts in habitat; however, it is worth noting that the 3 sightings of this species occurred in surveys conducted in the summer–fall period, in the deepest mean water depth, and at the greatest mean distance to land of any species observed in the study area (Table 6). Season, distance to shore, and depth of striped dolphin encounters correspond with those of previous surveys conducted in summer and fall and with habitat models that revealed the presence of striped dolphins in tropical to warm–temperate pelagic waters, with a continuous distribution outside upwelling coastal waters of California (Perrin et al., 1985; Jefferson et al., 1993; Mangels and Gerrodette, 1994; Archer and Perrin, 1999; Becker et al., 2012; Forney et al., 2012).

Short-finned pilot whales were encountered commonly off Southern California before the El Niño event in 1982–83 (Dohl et al.[1]); on the basis of numerous surveys, including this one, it is apparent that this species now uses these waters only infrequently (Carretta and Forney, 1993; Shane, 1994; Barlow[3]; Forney, 2007). The single encounter of false killer whales in the study area occurred during the 2008 winter cruise at a depth of 300 m and within 5 km of Santa Rosa Island. False killer whales are normally found in tropical to warm–temperate oceans; however, sightings have been made occasionally in cold–temperate areas as well (Stacey and Baird, 1991; Baird, 2008).

Conclusions

We collected sighting data from seasons and years that have not been reported previously, generated density and abundance estimates for 11 species of cetaceans off Southern California, and documented shifts in seasonal distribution for fin whales and Pacific white-sided dolphins. In recent years, interest has increased in the development of predictive models to forecast near real-time marine mammal distribution as a way to inform, mitigate, and decrease the effect of potentially harmful human activities in the marine environment (Becker et al., 2012; Forney et al., 2012; Thompson et al., 2012; Henderson et al., 2014). Although our data set spans a 5-year period that ends in 2008, visual and acoustic data on detections of marine mammals continue to be collected with corresponding oceanographic data, both physical and biological, during CalCOFI cruises. As the CalCOFI data set grows, it potentially could become one of the most valuable collections of data both for monitoring and creating year-round habitat models of cetacean species and their environment off Southern California.

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Population demographics of Hickory Shad (*Alosa mediocris*) during a period of population growth

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Abstract—Our study goal was to characterize the demographics of the population of Hickory Shad (*Alosa mediocris*) in the Albemarle Sound–Roanoke River watershed during a period of population increase and to assess its susceptibility to harvest. Adults were collected from gillnet surveys and a river recreational fishery from February to May 1996. The male-to-female ratio was similar between the Albemarle Sound (0.73:1) and the spawning grounds in Roanoke River (0.76:1). Ages were 2–7 years, but most sampled fish were age 3 or 4. The von Bertalanffy growth equation was $L_t = 460\ (1 - e^{-0.24(t + 1.63)})$, where L_t was predicted length at time t for sexes combined. Total mortality (Z) was 1.43 for males age 3–5, 1.76 for females age 4–6, and 1.40 for sexes combined. Sexual maturity in both sexes was essentially complete by age 4. Repeat spawning was common: 46.8% of males were virgin, 45.5% had spawned once, and 7.7% had spawned 2 or 3 times. For females, 24.9% were virgin, 45.5% had spawned once, and 29.6% showed evidence of spawning 2, 3, or 4 times. Mesentery fat in both sexes decreased from the prespawning aggregation (staging) area in the sound to the river spawning grounds, indicating that both sexes feed extensively in ocean waters before the inland portion of the spawning migration. The short lifespan of Hickory Shad, combined with an early age to maturity and an anadromous migration pattern, indicates that mature individuals are very susceptible to recreational and commercial harvest and are removed by exploitation or natural mortality within 1 or 2 seasons.

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Hickory Shad (*Alosa mediocris*) is 1 of 4 anadromous *Alosa* species native to the East Coast of North America. The other species are American Shad (*A. sapidissima*) and the river herrings Blueback Herring (*A. aestivalis*) and Alewife (*A. pseudoharengus*). Often, Hickory Shad is confused with American Shad, and they commonly appear together in local fish markets. Hickory Shad ranges from Cape Cod, Massachusetts, to the St. Johns River, Florida (Robins at al., 1986) and there is no evidence of spawning populations north of Maryland (Richkus and DiNardo[1]). It is assumed that this species returns to natal streams to spawn as does American Shad (Melvin et al., 1986), but homing has not been documented. Hickory Shad typically are 30–45 cm in fork length (FL) and 0.5–1.0 kg in weight—size ranges that are intermediate between the larger American Shad and smaller river herrings (Robins et al., 1986).

The center of abundance for Hickory Shad is thought to be in North Carolina because historically the North Carolina commercial fishery landed the greatest number of Hickory Shad among the fisheries along the U.S. eastern seaboard (Atlantic States Marine Fisheries Commission [ASMFC][2]). In 1902, the Hickory Shad harvest from North Carolina through Florida was 351,970 kg (775,962 lb) and worth $37,709 (approximately $900,000 in 2011 dollars); North Carolina fisheries landed 88.3% of the total and represented 90.0% of the dockside value (Alexander, 1905). By 2001, the species was an incidental catch in various North Carolina gillnet fisheries in Albemarle and Pamlico sounds and in the coastal Atlantic Ocean (North Carolina Division of Marine Fisheries [NCDMF][3]). Hickory Shad also were landed from pound nets, haul seines, and the nearshore ocean winter trawl fishery (Street et al.[4]).

[1] Richkus, W. A., and G. DiNardo. 1984. Current status and biological characteristics of the anadromous alosid stocks of the eastern United States: American shad, hickory shad, alewife, and blueback herring, 248 p. Atlantic States Marine Fisheries Commission, Washington, D.C.

[2] ASMFC (Atlantic States Marine Fisheries Commission). 1999. Amendment 1 to the interstate fishery management plan for shad and river herring. Fishery Management Report No. 35, 76 p. ASMFC, Washington, D.C. [Available from http://www.asmfc.org/uploads/file/shadam1.pdf.]

[3] NCDMF (North Carolina Division of Marine Fisheries). 2001. Assessment of North Carolina commercial finfisheries, 1997–2000. Final performance report for Award Number NA 76 FI 0286, segments 1–3, 365 p. [Available from Division of Marine Fisheries, North Carolina Department of Environment and Natural Resources, 3441 Arendell St., Morehead City, NC 28557.]

[4] Street, M. W., P. P. Pate, B. F. Holland Jr., and A. B. Powell. 1975. Anadromous fisheries research program, northern coastal region, North Carolina. Final report for Project AFCS-8, 210 p. Division of Marine Fisheries, North Carolina Department of Natural and Economic Resources, Morehead City, NC.

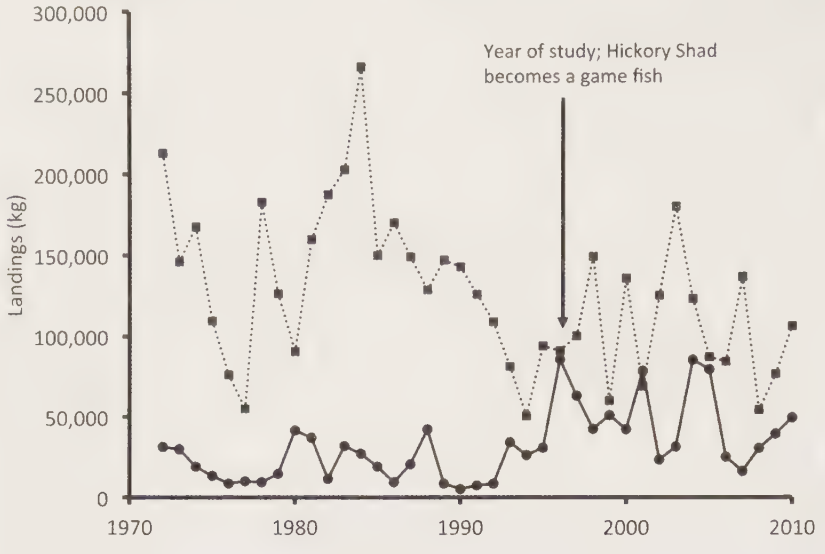

Figure 1

Commercial harvest of Hickory Shad (*Alosa mediocris*) and American Shad (*Alosa sapidissima*) in North Carolina for the period of 1972–2010. The study was conducted after a period of population growth for Hickory Shad from 1990 to 1996. Baseline data for the 20th century are those from 1890 (when landings of Hickory Shad were 104,780 kg [231,000 lb]) to 1902 (when landings had increased to 310,711 kg [685,000 lb] [Alexander, 1905]).

During the 1990s, Hickory Shad populations increased, whereas populations of the other 3 *Alosa* species of the eastern seaboard decreased (Rulifson, 1994; Waldman and Limburg, 2003; Watkinson, 2004). This trend was evident in the commercial landings data for North Carolina (Fig. 1). Federal and state landings data for shads are sometimes difficult to interpret because often Hickory Shad are not separated from landings of American Shad. However, personnel of state fisheries agencies and recreational fishermen have noted these increases through much improved springtime opportunities (e.g., catches and abundance) in the recreational fishery throughout the range of the Hickory Shad. In North Carolina and other mid-Atlantic states, sportfishing for Hickory Shad is now common during February, March, and April, when adults ascend rivers to spawn before the other 3 *Alosa* species; this shad is also popular as a secondary target in the spring sport fisheries for White Perch (*Morone americana*) and Striped Bass (*M. saxatilis*). The Roanoke River watershed just downstream of the last dam at Roanoke Rapids, North Carolina, and the tributary Cashie River near the town of Windsor are popular areas for Hickory Shad sportfishing (Fig. 2). Angler harvest in the Roanoke River watershed increased from a 1968 estimate of 143 Hickory Shad caught by rod and reel and 2377 fish caught by special devices, such as dip nets and gill nets (Baker[5]), to a 1996 estimate of 58,621 fish caught by hook and line that did not include the significant harvest by bank anglers (Kornegay[6]).

In 1996, concerns about overharvesting caused the North Carolina Wildlife Resources Commission (NCWRC) to classify Hickory Shad as a game fish in inland waters (Fig. 1). Since then, the bag limit has been 10 shads in aggregate per day (but only 1 American Shad) in inland, estuarine, and coastal waters (ASMFC[2]). Subsequently, the recreational fishery for Hickory Shad and Striped Bass in the Roanoke River has turned into a multimillion-dollar activity (McCargo et al.[7]). In 2006, anglers expended 14,065 hours (standard error of the mean [SE] 11,589), primarily in March and April. An estimated 81% of the shad were released; the remainder was harvested, but only 1.4% of that remainder were American Shad—indicating the importance of Hickory Shad to the sport fishery. Similar trends have been observed in the nearby Neuse River watershed, which has supported a long-standing shad sport fishery (Marshall, 1977; Hawkins[8]; Manooch, 1984).

A comprehensive review of Hickory Shad populations in South Atlantic coastal states was conducted by Rulifson et al. (1982), who documented that many of the life history aspects of this species were unknown. Since then, life history aspects of the Hickory Shad have been studied in Virginia rivers by Watkinson (2004), the Roanoke River by Batsavage (1997) and Harris and Hightower (2010, 2011), the Tar-Pamlico River by Smith (2006), Murauskas (2006), and Murauskas and Rulifson (2009, 2011), and the Neuse River by Burdick and Hightower (2006), al-

[5] Baker, W. D. 1968. A reconnaissance of anadromous fish runs into the inland fishing waters of North Carolina. Final report for Project AFS-3, 38 p. [Available from Division of Inland Fisheries, North Carolina Wildlife Resources Commission, 1751 Varsity Dr., Raleigh, NC 27606.]

[6] Kornegay, J. W. 1996. Unpubl. data. North Carolina Wildlife Resources Commission, 1751 Varsity Dr., Raleigh, NC 27606.

[7] McCargo, J. W., K. J. Dockendorf, and C. D. Thomas. 2007. Roanoke River recreational angling survey, 2005–2006. Final report, Coastal Fisheries Investigations, Federal Aid in Fish Restoration Project F-22, 67 p. [Available from Division of Inland Fisheries, North Carolina Wildlife Resource Commission, 1751 Varsity Dr., Raleigh, NC 27606.]

[8] Hawkins, J. H. 1980. Investigations of anadromous fishes of the Neuse River, North Carolina. Special Scientific Report. No. 34, 111 p. Division of Marine Fisheries, North Carolina Department of Natural Resources and Community Development, Morehead City, NC.

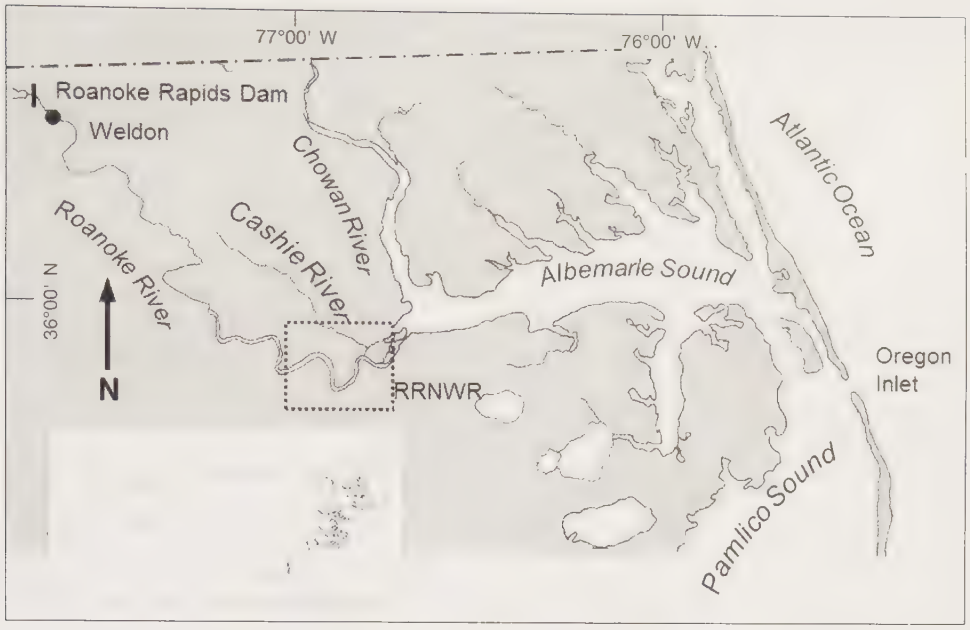

Figure 2

Map of the lower Roanoke River watershed and Albemarle Sound in North Carolina, showing the general locations where adult Hickory Shad (*Alosa mediocris*) were collected during February–May 1996 from 2 independent gillnet surveys in the western end of Albemarle Sound, in the Roanoke River National Wildlife Refuge (RRNWR; indicated with dotted rectangle), and in the recreational fishery on the spawning grounds of Hickory Shad near the city of Weldon, North Carolina.

though none except Batsavage (1997) were focused on age and growth. At the southern end of its range in Florida, the St. Johns River population was studied early by Walberg (1960) and Williams and Bruger[9]. In North Carolina, no directed sampling by state agencies has been conducted since 1993, but the NCWRC has collected Hickory Shad data for the 4 major North Carolina coastal rivers (Roanoke, Tar-Pamlico, Neuse, and Cape Fear) between 2000 and 2010 with annual monitoring (Dockendorf[10]).

Understanding key aspects of the life history, as well as the stock status of individual populations, is critical for species management. The ASMFC has long identified life history aspects and the stock status of Hickory Shad as priorities for future research (Richkus and DiNardo[1]; ASMFC[11,12,13]).

The goal of our study was to characterize the demographics of Hickory Shad during a known period of stock rebuilding with the Albemarle Sound–Roanoke River watershed as the focus population because of the important commercial and recreational fisheries there that target Hickory Shad. We describe the age, size, sex ratio, fecundity, age to maturity, growth, and mortality of adult Hickory Shad in the spring prespawning population in Albemarle Sound and during the spawning run near the spawning region in the Roanoke River near Weldon, North Carolina. Results of this study provide important life history information for future management plan development.

[9] Williams, R. O., and G. E. Bruger. 1972. Investigations on American shad in the St. Johns River. Technical Series No. 66, 49 p. Florida Department of Natural Resources, St. Petersburg, FL. [Available from http://research.myfwc.com/publications/publication_info.asp?id=29934.]

[10] Dockendorf, K. 2013. Personal commun. North Carolina Wildlife Resources Commission, Raleigh, NC 27606.

[11] ASMFC (Atlantic States Marine Fisheries Commission). 1985. Fishery management plan for the anadromous alosid stocks of the eastern United States: American shad, hickory shad, alewife, and blueback herring. Phase II in interstate management planning for migratory alosids of the Atlantic coast. Fisheries Management Report No. 6, 347 p. ASMFC, Washington, D.C. [Available from http://www.asmfc.org/uploads/file/1985FMP.pdf.]

[12] ASMFC (Atlantic States Marine Fisheries Commission). 2007. American shad stock assessment report for peer review, vol. 3. Stock Assessment Report No. 07-01 (Supplement), 489 p. ASMFC, Washington, D.C. [Available from http://www.asmfc.org/uploads/file/2007ShadStockAssmtReportVolumeIII.pdf.]

[13] ASMFC (Atlantic States Marine Fisheries Commission). 2009. Review of the Atlantic States Marine Fisheries Commission fishery management plan for shad and river herring (Alosa spp.) 2009, 11 p. ASMFC, Washington, D.C. [Available from http://www.asmfc.org/uploads/file/2009ShadFMPReview.pdf.]

Materials and methods

Study area

Albemarle Sound is an extensive estuarine habitat in northeastern North Carolina, measuring 88.5 km long east to west and 4.8–22.5 km wide north to south (Street et al.[4]; Fig. 2). Known spawning populations of Hickory Shad are located in 3 of the 15 tributaries—the Roanoke, Cashie, and Chowan Rivers—all of which are situated at the extreme western end of Albemarle Sound. The estuary is relatively shallow, with depths ranging from 5.5 to 7.6 m, and is bordered by cypress swamps and small sand beaches. The sound is essentially freshwater through its western and central portions and brackish in the eastern part. Access to the Atlantic Ocean is at Oregon Inlet between Bodie and Hatteras islands, which are parts of the Outer Banks barrier island system. The Roanoke River is the largest tributary to Albemarle Sound in terms of freshwater input. Only the last 220.5 km of the river are accessible to anadromous fishes; upriver portions are blocked by a series of impoundments ending with the Roanoke Rapids Reservoir upstream from Weldon (Rulifson and Manooch, 1991). The coastal plain portion of the watershed downstream of the last dam has an extensive floodplain that consists of hardwood forest, backwater swamps, oxbow lakes, and small creeks (Zincone and Rulifson, 1991), which are connected to the river by natural and anthropogenic openings in the natural river levee (Walsh et al., 2005).

Field collection

Adult Hickory Shad were collected during 2 independent gillnet surveys and the Roanoke River recreational fishery. Albemarle Sound and its tributaries were sampled in the NCDMF Independent Gill Net Survey of Albemarle Sound Striped Bass from 19 February to 1 May 1996. Anchored, experimental gill nets in both floating and sinking configurations were 36.6 m long and constructed of monofilament with stretched mesh sizes ranging from 64 to 178 mm in 13-mm increments; additional nets of 203-mm and 254-mm stretched mesh were also used (Dilday and Winslow[14]). The lower Roanoke River at the Roanoke River National Wildlife Refuge (RRNWR; Fig. 2) was sampled during an independent gillnet survey conducted by personnel from the National Marine Fisheries Service and RRNWR from 30 March to 17 April 1996. The single-mesh gill nets ranged from 3.6 m long and 1.5 m deep to 12.2 m long and 2.3 m deep; stretched mesh sizes ranged from 63 mm to 76 mm (Settle et al., 1996). During the spawning run, fish from the sport fishery at Weldon were obtained at access points (primarily boat ramps) and examined fresh; fish from the gillnet surveys were frozen and transported to the laboratory for examination. Each fish was measured for both FL and total length (TL) in millimeters and weighed to the nearest gram. Gonads were removed from the fresh fish and weighed to the nearest gram, and ovaries were preserved in 10% cold buffered formalin for later examination. Chi-square tests were used to determine significant differences in adult sex compositions between the 3 collection sites, and regression analyses were used to establish length-weight relationships.

Age analysis

Both scales and sagittal otoliths were used for aging adult Hickory Shad. From the left side above the lateral line and below the dorsal fin, 10–20 scales were removed. Scales were soaked in soapy water to remove dirt, mucus, and residual pigment and then dried. For examination under a microfiche reader equipped with a 24× lens, scales were mounted between 2 glass slides. Whole otoliths were removed, then aged by placing each in a watch glass containing distilled water and viewed under a dissecting microscope at 30× magnification. Otoliths were not sectioned for aging because their thin nature allowed their rings to be visible on their external portions.

Both scales and otoliths were aged by 3 independent readers; each determination was considered successful when either the scale or otolith ages of at least 2 readers agreed. For scale aging, the traditional techniques and criteria of Cating (1953), Judy (1961), Street and Adams[15], and Pate (1972) were used. Otolith aging techniques used criteria by Kornegay (1977) and Libby (1985). Results for fish aged with both scales and otoliths were used to determine agreement between the 2 aging methods.

Otoliths were used to back calculate growth because erosion of scale margins during the spawning migration precludes the necessary relationship between fish length and scale radius (DeVries and Frie, 1996). To determine the relationship of otolith radius to FL, we used 75 fish, of which all fish <250 mm FL and nearly all fish >350 mm FL; 8 of those larger fish had otoliths that were unreadable. The 2 dominant length classes (250–299 and 300–349 mm FL) were subsampled to minimize bias associated with the effect that dominant size classes can have on linear regression calculations. Otolith images were measured on a video screen connected to a dissecting microscope at 16× power; otolith annuli were measured vertically from the nucleus to the ventral margin.

[14]Dilday, J. L., and S. E. Winslow. 2000. North Carolina striped bass monitoring. Annual report, Grant F-56, segment 7, 43 p. [Available from Division of Marine Fisheries, North Carolina Department of Environment and Natural Resources, 3441 Arendell St., Morehead City, NC 28557.]

[15]Street, M. W., and J. G. Adams. 1969. Aging of hickory shad and blueback herring in Georgia by the scale method. Contribution Series No. 18, 13 p. Marine Fisheries Division, Georgia Game and Fish Commission, Brunswick, GA.

Two separate methods were used to estimate length at age. FL at age was estimated from the von Bertalanffy growth equation (Cailliet et al., 1986), which was calculated with mean back-calculated FL at age (sexes combined). Back calculations also were computed by the Dahl-Lea direct proportion method (DeVries and Frie, 1996) with the following equation:

$$L_i = (S_i / S_c)\, L_c, \quad (1)$$

where L_i = back-calculated FL (mm) of the fish at formation of the i^{th} increment;
L_c = FL (mm) at capture;
S_c = otolith radius at capture; and
S_i = otolith radius at the i^{th} increment.

Mortality estimates

Mortality was estimated for ages where recruitment was more than 95% complete (on the basis of catch curves)—for males ages 3–5, females ages 4–6, and sexes combined ages 3–6 to eliminate age classes not fully recruited to the spawning population. Total instantaneous mortality (Z) was calculated by least-squares regression, and by estimating the slope of the line from the catch curve of a single season. Annual total mortality (A) was estimated by taking the inverse natural log of $-Z$ and subtracting the value from 1 (Ricker, 1975):

$$A = 1 - e^{-Z}. \quad (2)$$

Spawning history

Spawning history for both sexes was determined by counting the number of spawning marks on the scales; spawning marks are formed by erosion of the scale margin from lack of feeding during the spawning migration (Cating, 1953; Pate, 1972). Spawning marks are thicker and more visible than the winter annuli that form before a fish matures sexually. The presence of these marks on scales is indicative of repeat spawners in a population, and the percentage of repeat spawners can be calculated. The percentage of the population that was sexually mature was calculated by sex by dividing the number of fish with developed gonads by the total number of fish examined.

Fecundity and gonadosomatic index

When this research was completed in 1996, gonadal maturity and fecundity were not well understood. We understand now that the Hickory Shad is a batch spawner (Murauskas and Rulifson, 2011), a characteristic that requires special consideration in the estimation of fecundity (Olney et al., 2001; Murua and Saborido-Rey, 2003). However, in 1996, sexual maturity was assigned by visual inspection of the gonads. We present the gonadosomatic index (GSI) here as documentation and for comparison with other limited studies of this species in other watersheds. For sexually mature individuals, the number of ova present in each ovary was estimated by the gravimetric method.

Each preserved whole ovary was blotted with a wet paper towel and then weighed to the nearest 0.01 g. Three subsamples of ovarian tissue, each ~0.50 g, were taken from each ovary at the anterior, medial, and posterior regions. Each subsample was weighed, the ova were counted, and the number of ova per gram of ovarian tissue was calculated. The mean number of ova present in the 3 subsamples was multiplied by ovary weight to estimate the total number of ova in that ovary; the sum of the ova in the 2 ovaries was considered the estimate of total potential fecundity. The GSI was estimated by dividing the gonad weight by somatic body weight (no gonads or gastrointestinal tract),and then multiplying the quotient by 100. The mean GSI was calculated by week so that temporal changes in the GSI could be identified. Two-sample t-tests with assumed unequal variances were used to detect differences between left and right ovaries in weight and total counts of ova. To detect significant differences in the number of ova per gram of ovarian tissue between the 3 regions of the ovary, analysis of variance was performed with Statistical Analysis System[16] software. Regression analysis was used to predict potential fecundity on the basis of FL, somatic weight, and age. Significance was assigned an alpha (α) value of 0.05.

Mesentery fat and gut content analyses

The few literature references available on this topic indicate that Hickory Shad usually do not feed during the spring spawning migration (White and Curtis[17]; Curtis[18]; Perkins and Dahlberg, 1971; Pate, 1972; Harris et al., 2007). However, we observed Hickory Shad in the Roanoke River (during this study) and Neuse River (Murauskas and Rulifson, 2011) with full stomachs, and Harris et al. (2007) found similar trends in the St. Johns River population. To determine whether feeding or fat reserves were more important during the phase of inland spawning migration, we removed mesentery fat from the viscera and weighed it to the nearest 0.01 g. Food items removed from the stomach and intestine were identified to the lowest practical taxon, enumerated, and weighed to the nearest 0.01 g. T-tests were used to test for significant differences in mesentery fat between males and females and between fish collected in Albemarle Sound and fish collected in the Roanoke River. Relationships between mesentery fat and somat-

[16]Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

[17]White, M. G., III, and T. A. Curtis. 1969. Anadromous fish survey of the Black River and Pee Dee River watersheds. Project AFS-2-4, 73 p. South Carolina Wildlife Resources Department, Charleston, SC.

[18]Curtis, T. A. 1970. Anadromous fish survey of the Ashley River watershed. Project AFS-2, 91 p. South Carolina Wildlife Resources Department, Charleston, SC.

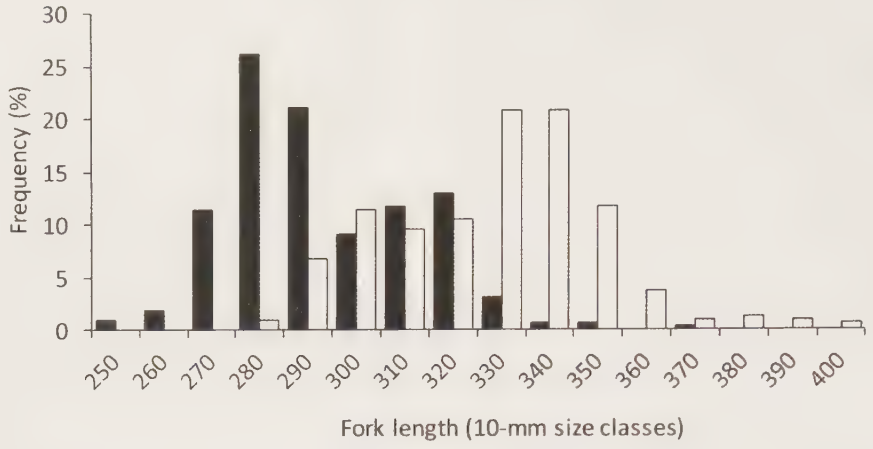

Figure 3

Length-frequency distributions for male (black bars) and female (white bars) Hickory Shad (*Alosa mediocris*) collected from the Albemarle Sound–Roanoke River watershed in North Carolina during the spawning run in the spring of 1996. Frequencies are expressed as percentages, and fork lengths are delineated in 10-mm increments.

ic weight and between mesentery fat and gonad weight were estimated by regression analyses.

Results

Sex ratios, lengths, and age

The male-to-female ratio of 0.73:1(n=266) for Albemarle Sound was similar (χ^2=0.064, n=532, df=1, P>0.05) to the ratio for the spawning grounds on the Roanoke River at Weldon (0.76:1, n=266). Although there were more female Hickory Shad collected in the Albemarle Sound than on the spawning grounds in the river, the sex ratios were similar at both areas; however, in the RRNWR, the sex ratio was significantly skewed toward males. The independent gillnet survey conducted in the RRNWR was biased by the gear characteristics used (e.g., mesh sizes), yielding a male-to-female ratio of 4.29:1 (n=111)—a value significantly different from that of the other 2 sites (χ^2=54.28, n=643, df=2, P<0.001). The mean size and range of lengths were larger for females than for males. Females were 280–402 mm FL, and males were 257–376 mm FL. Dominant size classes (10-mm increments) were 330–339 and 340–349 mm FL for females (41.5%) and 280–289 and 290–299 mm FL for males (47.3%) (Fig. 3).

Body weight, or Log_e body weight (BWT) measured in grams, increased with length, or Log_e FL measured in millimeters, for both males (coefficient of determination [r^2]=0.78) and females (r^2=0.73). The following equations were used to calculate these relationships:

$$\text{Males: } \log_e BWT = 3.09(\log_e FL) - 11.76; \text{ and} \quad (3)$$

$$\text{Females: } \log_e BWT = 2.94(\log_e FL) - 10.80. \quad (4)$$

Because gonad weight varied considerably for both sexes, the length-weight relationship was calculated for somatic weight ($\log_e SWT$), improving the linear fit for males (r^2=0.81) and females (r^2=0.76). The following equations were used to determine these relationships:

$$\text{Males: } \log_e SWT = 3.01(\log_e FL) - 11.34; \text{ and} \quad (5)$$

$$\text{Females: } \log_e SWT = 2.78(\log_e FL) - 9.98. \quad (6)$$

As expected, the relationship between FL and TL was highly correlated (r^2=0.99). The following equation was used to establish this relationship:

$$\text{Log}_e TL = 0.99(\log_e FL) + 0.19. \quad (7)$$

Ages determined from scales and otoliths showed only a 57% agreement (n=478 pairs). On the basis of results of similar otolith–scale comparisons reported for Hickory Shad (Murauskas, 2006) and for other species (e.g., Kornegay, 1977; Paramore, 1998; Paramore and Rulifson, 2001), we assumed that otolith ages were accurate. With that assumption, scales generally overestimated the age of younger fish and underestimated the age of older fish (Table 1). However, scale and otolith ages never differed by more than 2 years for any given fish. There was no agreement between age-2 scales and otoliths. Agreement of age-3 scales and otoliths was 62%, age-4 scales and otoliths had a 61% agreement, and only 26% of scales age 5 and older agreed (Table 1).

Table 1

Percent agreement of ages, measured in years, from scales and otoliths of Hickory Shad (*Alosa mediocris*) collected in Albemarle Sound from February to May 1996. Data represent percent agreement calculated with otolith age as the standard; bold numbers indicate one-to-one correspondence (100% accuracy).

Otolith age	Scale age						Total number of otoliths examined
	2	3	4	5	6	7	
2	**0**	65	35	0	0	0	20
3	4	**62**	30	4	0	0	242
4	0	23	**61**	15	1	0	192
5	0	15	55	**25**	5	0	20
6	0	0	0	0	**50**	50	2
7	0	0	0	0	50	**50**	2
Total number of scales examined	10	209	208	44	5	2	478

Because of the deciduous nature of *Alosa* scales, otoliths were used for age composition analyses, mortality estimates, and back calculations of length at age. Scales that agreed in age with their respective otoliths were used for spawning mark analysis.

The Hickory Shad population in the Albemarle Sound and Roanoke River ranged from age 2 to age 7, but the majority were age-3 and age-4 fish (Table 2). Age-3 males were dominant (66%), and the majority of females (55%) were age 4. Females were larger at age than were males, but size ranges (Table 2) and weights (Table 3) at age for each sex showed some degree of overlap.

There was a strong relationship between otolith radius and FL. The following equations were used to express this relationship:

$$\text{Males: } FL = 133.32(\textit{otolith radius}) - 62.35, \quad (r^2 \text{ [coefficient of determination]}=0.95); \tag{8}$$

$$\text{Females: } FL = 116.54(\textit{otolith radius}) - 31.18, \quad (r^2=0.92); \text{ and} \tag{9}$$

$$\text{Sexes combined: } FL = 117.02(\textit{otolith radius}) - 29.20, \quad (r^2=0.93). \tag{10}$$

The von Bertalanffy growth equation was

$$L_t = 460\ (1 - e^{-0.24(t + 163)}). \tag{11}$$

In general, the mean back calculations of length at age were shorter than the observed lengths for younger fish and longer than observed lengths for older fish (Table 2). With the proportional method, back-calculated lengths for male Hickory Shad of ages 2–4 were shorter

Table 2

Observed means and ranges of fork lengths at age, measured in millimeters and years, respectively, and back-calculated estimates of fork lengths at age of male and female Hickory Shad (*Alosa mediocris*) collected from the Albemarle Sound–Roanoke River watershed in 1996. Sexes combined represent the predicted size-at-age from the von Bertalanffy growth function (VBGR). Standard deviations (SD) are provided in parentheses. *n*= number of fish sampled.

Age	Males				Females				Sexes combined (VBGR)
	n	Mean (SD)	Range	Calculated	*n*	Mean (SD)	Range	Calculated	
1	0			206	0			212	215
2	16	293 (9.3)	278–314	247	9	304 (7.0)	292–313	263	268
3	178	288 (12.9)	257–328	287	78	313 (18.4)	280–360	306	309
4	69	319 (11.9)	283–354	293	133	339 (15.3)	296–390	345	341
5	4	332 (16.4)	318–355	355	18	343 (18.8)	320–397	363	366
6	1	376			1	402		402	386
7	0				2	397 (4.2)	394–400	394	402
Total	268				241				

Table 3

Observed means and ranges of body and somatic weights at age, measured in grams and years, respectively, of male and female Hickory Shad (*Alosa mediocris*) collected from the Roanoke River–Albemarle Sound watershed in 1996. Standard deviations (SD) are provided in parentheses. *n*=number of fish sampled.

	Males					Females			
	Body weight		Somatic weight			Body weight		Somatic weight	
Age	*n*	Mean	Range	Mean	Range	*n*	Mean	Range	Mean	Range
2	16	330 (41.7)	273–411	310 (35.8)	256–388	9	391 (27.3)	358–446	343 (15.8)	325–379
3	178	319 (54.1)	210–548	300 (57.8)	197–525	78	440 (85.4)	291–839	390 (71.1)	280–612
4	69	451 (70.2)	316–698	422 (59.8)	297–640	133	591 (101.1)	359–839	505 (83.2)	318–705
5	4	452 (65.2)	403–542	430 (69.6)	385–532	18	639 (113.9)	447–908	542 (84.6)	417–710
6	1	651		638		1	1031		871	
7						2	946 (192.0)	810–1082	779 (145.4)	676–881
Total	268					241				

and lengths for age-5 males were longer than observed values. Females were similar to males except for age-7 fish, which had back-calculated lengths that were shorter than observed values. Predicted FL values from the von Bertalanffy growth equation were less than the observed lengths for age-2 fish and greater than the observed lengths for fish of ages 5–7. Predicted lengths for age-3 and age-4 fish fell between the mean observed lengths for age-3 and age-4 males and females (Table 2). Females were larger and heavier at age than males (Tables 2 and 3).

Mortality, maturity, and fecundity

Mortality estimates were lower for males than for females. Total instantaneous mortality (Z) was 1.43 for males of ages 3–5, 1.76 for females of ages 4–6, and 1.40 for both sexes combined. Annual total mortality (A) was 0.76 for males, 0.83 for females, and 0.75 for both sexes combined. Between 36% and 38% of both male and female Hickory Shad were sexually mature by age 2, most (>93%) were mature by age 3, and almost all were mature by age 4 (Table 4). Virgin males represented 46.8% of the male population; an additional 45.5% had spawned once, and 7.7% had spawned at least 2 or more times (Table 4). No males exhibited more than 3 spawning marks. Virgin females composed only about one-fourth (24.9%) of the sample, 45.5% of females had spawned once before, and 29.1% of them showed evidence of spawning 2 or 3 times. One age-7 female had 4 spawning marks (Table 4).

Slowly increasing trends in the mean GSI were observed for Hickory Shad from both Albemarle Sound and Roanoke River through March, whereas mean GSI slowly decreased through the week of April 7–13 and then decreased quickly thereafter (Fig. 4). The mean number of ova per gram of ovarian tissue ranged from more than 1500 to less than 4000, and the anterior portions of both ovaries tended to have higher ova counts per gram of ovarian tissue than the posterior region. This relationship was significant for the left ovary (n=47, F=4.68, P=0.011) but not for the right ovary (F=1.21, P=0.303). The left ovary was significantly greater in weight and mean total egg counts than the right ovary (n=186, t=3.686, P<0.001). Mean left ovary weight was 42.88 g, and mean right ovary weight was 35.98 g. Mean left egg count was 111,037, and the right ovary contained an average of 93,630 ova. These means were not significantly different for the left and right ovaries (n=47, t=–1.746, P=0.840). Potential fecundity (PF) of female Hickory Shad generally increased with fish length, body weight, somatic weight, and age class (Table 5). Fecundity estimates ranged from 80,290 to 478,944 ova (n=47). We used the following prediction equations:

$$\text{Log}_e PF = 3.90(\text{log}_e FL) - 10.46 \ (r^2=0.63); \quad (12)$$

$$\text{Log}_e PF = 1.33(\text{log}_e BWT) + 3.70 \ (r^2=0.76); \quad (13)$$

$$\text{Log}_e PF = 1.39(\text{log}_e SWT) + 3.59 \ (r^2=0.67); \text{ and} \quad (14)$$

$$\text{Log}_e PF = 0.30(Age) + 10.97 \ (r^2=0.52) \quad (15)$$

Feeding and mesentery fat

Fish collected from the Roanoke River had significantly less mesentery fat reserves than Albemarle Sound fish (males: n=62, t=–3.050, P=0.005; females: n=110, t=–4.54, P<0.0001). Also, male fish from the Roanoke River had significantly less remaining fat than Roanoke River females (n=98, t=–2.140, P=0.030), but this sex difference was not observed for fish collected in Al-

Table 4

Proportion (%) of mature fish by sex, determined from visual inspection of gonads, and number of spawning marks by age class for male and female Hickory Shad (*Alosa mediocris*) collected from the Roanoke River–Albemarle Sound watershed in 1996. *n*=number of fish examined.

	Males						Females						
		Number of spawning marks						Number of spawning marks					
Age	Percent mature	0	1	2	3	*n*	Percent mature	0	1	2	3	4	*n*
2	36.1	12				12	38.5	7					7
3	97.9	92	56			148	93.9	38	24				62
4	99.6	4	50	14		68	98.6	6	69	48			123
5	100	1	0	1	2	4	100	2	4	9	3		18
6	100	0	0	0	1	1	100	0	0	0	1	0	1
7							100	0	0	1	0	1	2
n examined	233	109	106	15	3	233	213	53	97	58	4	1	213
Proportion (%) of total population		46.8	45.5	6.4	1.3			24.9	45.5	27.2	1.9	0.5	

bemarle Sound (n=74, t=–1.570, P=–0.120), indicating that both sexes feed extensively in ocean waters before entering the phase of inland spawning migration. There were weak positive relationships between somatic weight and mesentery fat for both males (r^2=0.17) and females (r^2=0.29) in the Albemarle Sound, but these relationships essentially disappeared (males: r^2=0.14; females: r^2=0.02) on the spawning grounds in the Roanoke River (Fig. 5).

Interestingly, a similar set of relationships was observed between gonad weight and mesentery fat in males and females (males: R^2=0.46; females: R^2=0.21) in the Albemarle Sound—relationships that disappeared (males: R^2=0.20; females: R^2=0.05) on the spawning grounds (Fig. 6), indicating that fish were using mesentery fat during their upstream migration for metabolic energy and not for increasing gonad size.

For gut analysis, the stomachs of 212 fish were examined. Of the fish collected from the Albemarle Sound and Roanoke River, 26% (62) and 28% (110), respectively, contained identifiable items. In fish from both locations, 83% of stomach items found fitted into 5 categories: fish (Clupeidae), parasites (Isopoda), seeds, wood, and plastic. Insects, a sixth category, were found only in stomachs of Roanoke River fish.

Discussion

Adult sex ratios

The sex ratios in our study indicated that there was no sex-selective harvest by anglers in 1996. The male-to-female ratios from near the Roanoke River spawning grounds at Weldon (0.76:1) indicated that slightly more females than males were sampled. A similar result (0.73:1) was obtained from the NCDMF Independent Gill Net Survey of Striped Bass in the Albemarle Sound , but the independent gillnet survey in the RRNWR selected for male fish (4.29:1). The RRNWR survey used small mesh sizes, causing bias toward smaller males; the gillnet survey in Albemarle Sound for Striped Bass used a wide range of mesh sizes to allow for collection of the full size range of both sexes.

In some cases, males were more abundant than females because a greater proportion of males reach maturity at an earlier age; moreover, differential arrival periods of males and females on the spawning grounds, as in the Chesapeake Bay, can affect the sex ratios found in samples (Klauda et al. 1991a). Pate (1972) found the male-to-female ratio to be 4:1 for Hickory Shad sampled by a nonselective haul seine in the Neuse River, North Carolina. This ratio could have been the result of recruitment of a large proportion of virgin males to the spawning population (47.3% of the males were age 2).

Skewness of true sex ratios from increased mortality of a targeted sex likely plays a role in population rebuilding. For *Alosa* species, females are obviously the limiting factor, and older age classes have greater reproductive potential. Higher rates of survival to repeat-spawning age and a sex ratio closer to 1:1 should lead to accelerated population rebuilding, as opposed to the rebuilding potential of a population with far more males and virgin spawners. Some alosine fisheries (e.g., American Shad) target females for their roe (Rulifson et al., 1982), and such activity will shift the true sex ratio.

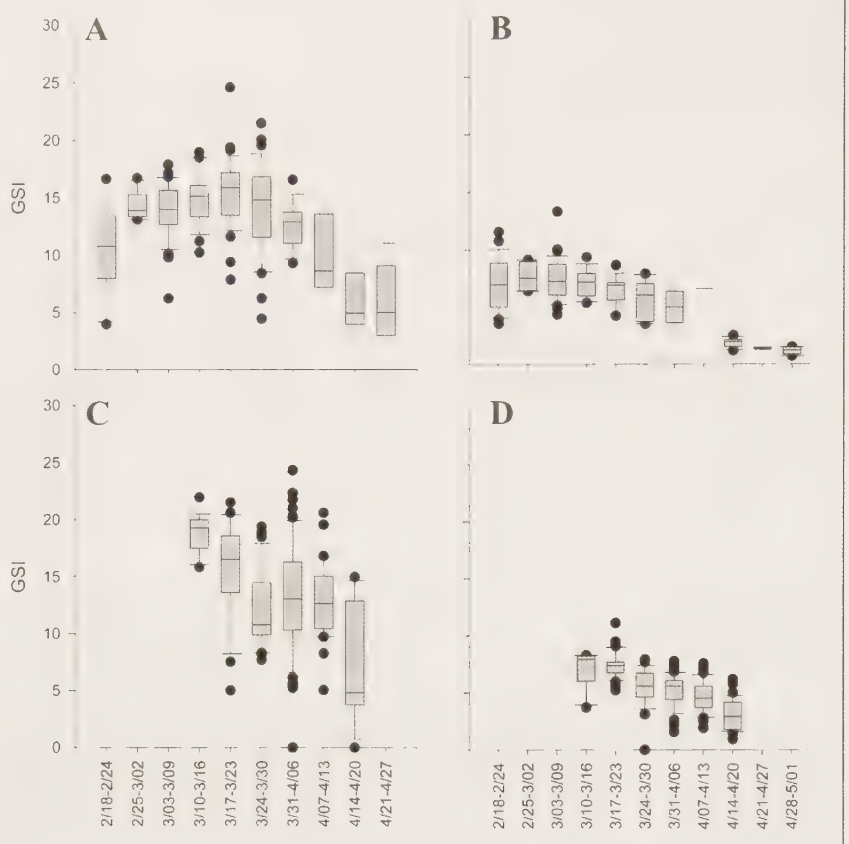

Figure 4

The mean (dashed line), median (solid line), 5–95% percentiles (box), 10th and 90th percentiles (whiskers), and outliers (dots) of gonadosomatic index (GSI) values for Hickory Shad (*Alosa mediocris*) collected during the prespawning and spawning periods during February–May 1996: (**A**) females and (**B**) males sampled from the Albemarle Sound as part of the North Carolina Divison of Marine Fisheries Independent Gill Net Survey and (**C**) females and (**D**) males from the Roanoke River sampled as part of a gillnet survey in the Roanoke River National Wildlife Refuge and from a recreational fishery at sites near the city of Weldon, North Carolina.

Age analysis, otolith back calculations, and mortality estimates

The 57% agreement between scale and otolith ages in our study in the Albemarle Sound–Roanoke River watershed is similar to results reported by Harris et al. (2007), who found a 57.3% agreement for fish from St. Johns River; 96% of the ages were in agreement of one year. Our study found no more than 2 years disagreement for any given fish. Kornegay (1977) reported a similar agreement for Alewife from Albemarle Sound, but for Blueback Herring his agreement was approximately 68%. Kornegay's (1977) Alewife scale ages never deviated by more than 2 years from otolith ages, but, for 2 Blueback Herring, scale ages deviated by up to 3 years from otolith ages.

A difference of 1 or 2 years between scale age and otolith age is a relatively large deviation for a fish with a lifespan of only 7 or 8 years. Likewise, the agreement level of 57% between scale and otolith ages is low. *Alosa* scales are commonly regenerated, and spawning marks sometimes obscure annuli near the scale margin. The first annulus is sometimes confused with the freshwater zone, which is a false annulus formed when juvenile *Alosa* first enter the marine environment, and the first annulus is not always visible on the scale (Cating, 1953; Judy, 1961; Kornegay, 1977). In addition, the Hickory Shad, among *Alosa* species, has scales considered to be the most difficult to use for age analysis (Richkus and DiNardo[1]). Therefore, otoliths should be used whenever possible for aging Hickory Shad.

The few published studies on age composition of Hickory Shad and other *Alosa* species generally show 1–3 dominant year classes (Street and Adams[15]; Pate, 1972; Street et al.[4]; Kornegay, 1977; Winslow[19,20]; NCDMF[21]; Harris et al., 2007). In our study, ages 3 and 4 were the dominant age classes, with male Hickory Shad contributing the majority of the younger age classes (ages 2 and 3) and female Hickory Shad contributing the majority of the older age classes (ages 4–7) (Table 2). For the adjacent Neuse River, Murauskas and Rulifson (2011) reported that both sexes averaged 3 years of age, although a larger proportion of females were in older age classes: 25% of females were of ages 4, 5, and 6, whereas 14% of males were of age 4 only.

Overlapping lengths at age made it difficult to accurately determine age structure from length fre-

[19]Winslow, S. E. 1989. North Carolina alosid fisheries management program. Completion report for Project AFC-27, 102 p. Division of Marine Fisheries, North Carolina Department of Natural Resources and Community Development, Morehead City, NC.

[20]Winslow, S. E. 1990. Status of American Shad, *Alosa sapidissima* (Wilson), in North Carolina. Completion report for Job 5, Project AFC-27, 94 p. + appendix. Division of Marine Fisheries, North Carolina Department of Natural Resources and Community Development, Morehead City, NC.

[21]NCDMF. 2001. North Carolina shad and river herring compliance report, 2000, 66 p. [Available from Division of Marine Fisheries, North Carolina Department of Environment and Natural Resources, 3441 Arendell St., Morehead City, NC 28557.]

quencies. Other studies on Hickory Shad and other *Alosa* species also showed a significant degree of overlap of lengths at age (Street and Adams[15]; Pate, 1972; NCDMF[21]). Our results indicate that the mean FLs at age for both sexes from age 3 and older were smaller than the means reported from earlier investigations. This difference could be the result of 1) the capture method used by previous investigators, who collected Hickory Shad in gill nets with large mesh sizes that were set for American Shad (Street et al.[4]; Hawkins[8]), 2) the scales used for determining age, or 3) both. Pate (1972) examined Hickory Shad captured in a nonselective haul seine and found that the largest Hickory Shad of both sexes were the oldest fish sampled (ages 5–7).

Table 5

Number of ova, estimated gravimetrically and from regressions developed for age, in ovaries of female Hickory Shad (*Alosa mediocris*), collected in Albemarle Sound and the Roanoke River in 1996, and mean values of the following variables: fork length (FL) measured in millimeters, body weight (BWT) measured in grams, and somatic weight (SWT) measured in grams at age, measured in years. *n*=number of ovaries examined.

Age	*n*	Gravimetric counts (observed)	Counts on basis of age	Counts by mean FL at age	Counts by mean BWT at age	Counts by mean SWT at age
2	1	85,803	108,012	138,195	113,366	121,109
3	14	137,523	147,267	154,849	132,642	144,776
4	19	223,576	200,787	211,380	196,382	207,344
5	3	294,798	273,758	221,275	217,874	228,758
6	1	478,944	373,249	410,929	411,646	442,326
7	2	250,918	508,897	391,352	367,134	378,751

The mean FLs from back calculations with both the Dahl-Lea direct proportion method and the von Bertalanffy growth equation indicate that the smaller age-2 Hickory Shad were not part of the spawning migration. The largest differences between mean observed FLs and mean back-calculated FLs from the von Bertalanffy growth equation occurred at age 2 (Table 2). The only age-2 fish sampled were the ones that were sexually mature. Analysis of spawning marks showed that approximately 41% of age-2 Hickory Shad (sexes combined) were mature at this age, indicating that the majority of age-2 Hickory Shad were not sampled. It is presumed that age-1 fish and many age-2 fish remain at sea, but this portion of the lifecycle is unknown.

Annual mortality rates were higher in this study (0.75, sexes combined) than in previous studies in Albemarle Sound; rates from other studies ranged from 0.40 to 0.65 (Street et al.[4]; Johnson et al.[22]). However, it should be noted that the annual mortality in those studies was calculated with the Robson and Chapman (1961) method that computes survival instead of using the catch curve to estimate mortality. Our mortality rates were higher for females (0.83) than for males (0.76). Because the catch curve was generated from just 1 year of data, it is difficult to determine the cause for higher mortality estimates. Moderate fluctuations in annual recruitment are common in fish populations, but catch curves derived from 2 or more years of data can reduce the effects of variable recruitment (Ricker, 1975).

Spawning history and reproductive analysis

The short lifespan of Hickory Shad, combined with an early age to maturity and an anadromous migration pattern, indicates that adult fish in the Albemarle Sound–Roanoke River population are subject to recreational (sound and inland waters) and commercial harvest (sound and ocean waters) for 1 or 2 seasons before they are removed by harvest or natural mortality. Approximately one-third of both sexes are sexually mature as early as age 2, >93% of the population is mature by age 3, and essentially 100% of the population is mature by age 4 (Table 4). One or 2 spawning marks on the scales examined were common, but 3 or more marks were rare. These results were similar to findings for Hickory Shad in the Altamaha River, Georgia (Street, 1970), the Neuse River (Pate, 1972), and more recently the Tar-Pamlico River (Murauskas and Rulifson, 2011).

On the basis of age to maturity and spawning patterns, Hickory Shad and American Shad are exploited similarly in the Albemarle Sound region, but the level of exploitation for these species differs south of Cape Hatteras. American Shad in Albemarle Sound usually reach sexual maturity by age 3 or age 4 for males and by age 4 or age 5 for females. Both sexes spawned up to 3 times (Winslow[19,20]). American Shad show a latitudinal gradient between semelparity and iteroparity throughout its range (Leggett and Carscadden, 1978). In contrast, individual American Shad in populations south of Cape Hatteras seldom spawn more than once, and adults in populations in New York and Connecticut

[22]Johnson, H. B., D. W. Crocker, B. F. Holland Jr., J. W. Gilliken, D. L. Taylor, M. W. Street, J. G. Loesch, W. H. Krete Jr., and J. G. Travelstead. 1978. Biology and management of mid-Atlantic anadromous fishes under extended jurisdiction. Completion Report AFCS-9-2, 175 p. Division of Marine Fisheries, North Carolina Department of Natural Resources and Community Development, Morehead City, NC, and Virginia Institute of Marine Science, Gloucester Point, VA.

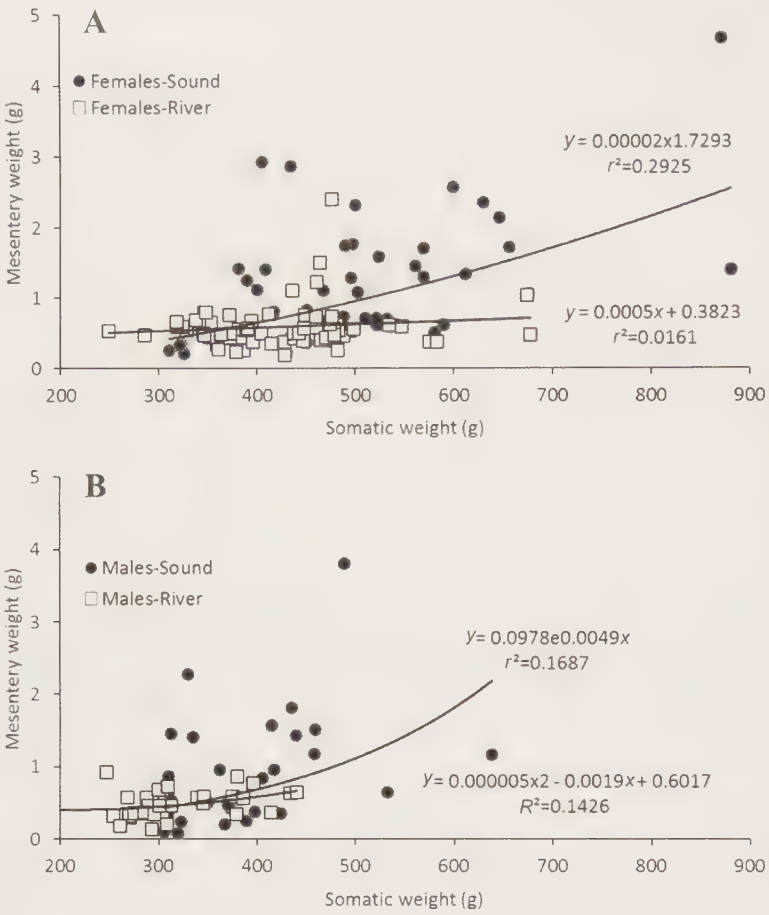

Figure 5

Relationship between mesentery fat and somatic weight, both measured in grams, of (**A**) female and (**B**) male Hickory Shad (*Alosa mediocris*) collected during February–May 1996 in Albemarle Sound and on the Roanoke River spawning grounds near Weldon, North Carolina. r^2=coefficient of determination; R^2=coefficient of multiple determination.

spawn up to 5 times. Hickory Shad appear to be iteroparous south of Cape Hatteras as indicated by repeat spawners in the Neuse River (Pate, 1972; Hawkins[8]), Altamaha River (Street, 1970), and St. Johns River (Harris et al., 2007). Because of the short life spans and limited number of spawning events (i.e., repeat spawning) exhibited by Hickory Shad and other *Alosa* species, successive years of poor recruitment could result in relatively quick population declines. Therefore, our estimate of 0.75 for annual total mortality, sexes combined, is possible. State landings data for Hickory Shad after 1996 indicate that such a mortality estimate may have been real (Fig. 1). Landings stabilized in the 2000s decade.

Mean GSI values were similar between fish caught in the Albemarle Sound and fish captured in the Roanoke River. The spawning season for Hickory Shad in the Albemarle Sound–Roanoke River watershed lasts for about 4 weeks in March and April; therefore, female Hickory Shad will be at differing degrees of gonadal development (i.e., prespawning, running ripe, partially spent, postspawning) for any given week during the spawning season, and this variation will result in a large variability in GSI values (Fig. 4). Murauskas and Rulifson (2011) observed multiple batch spawning of Hickory Shad in the Tar-Pamlico River watershed over several weeks, and these events were related to water temperature. This observation is supported by our ovary data, which revealed significantly different states of maturity between anterior and posterior oocytes in the ovaries.

Fecundity estimates are important in population modeling and also for hatchery managers who attempt to spawn and rear Hickory Shad for the purpose of stock restoration. The Maryland Department of Natural Resources has been rearing and stocking larval and early juveniles of both Hickory Shad and American Shad in at least 6 Chesapeake Bay watersheds and tributaries (Richardson et al.[23]). Although Olney et al. (2001) and Murauskas and Rulifson (2011) classified both species as batch spawners, Maryland hatchery personnel do not mention this aspect in their methodology. Both males and females received an intramuscular implant of leutinizing-hormone-releasing hormone analog (LHRHa) in the dorsal musculature at the collection site and were returned to the hatchery for spawning. Very little information exists on fecundity estimates of Hickory Shad, and estimates include age-2 fish. Pate (1972) reported 44,556 to 347,610 eggs per female from the Neuse River. Hickory Shad in the Altamaha River showed increased fecundity with age and size, with estimates ranging from 252,693 to 730,213 eggs per female and a mean of 500,519 eggs per female (Street, 1970). St. Johns River females exhibited low correlation between fecundity and weight, length, and age. Fecundity ranged from 168,000 to 591,000 eggs per female with a mean of 363,000 eggs per female (Williams and Bruger[9]). Our study of the Roanoke River population (egg counts from

[23]Richardson, B. M., C. P. Stence, M. W. Baldwin, and C. P. Mason. 2009. Hickory shad restoration in three Maryland rivers. F-57 Segment 9 Progress Report, 48 p. Maryland Department of Natural Resources, Oxford, MD. [Available from http://www.dnr.state.md.us/irc/docs/00014544.pdf.]

80,290 to 478,944) found good correlation of egg counts with weight, length, and age (Table 5).

It appears that suitable spawning habitats differ among watersheds. Spawning activity of Hickory Shad in the Neuse River, North Carolina, and the Altamaha River, Georgia, was confined primarily to flooded bottomlands and tributaries away from the main stem of each river (Street, 1970; Pate, 1972; Burdick and Hightower, 2006). Smith (2006) noted Hickory Shad spawning in small tributaries of the Tar-Pamlico River watershed. Mansueti (1962) found Hickory Shad spawning in the main stem of the Patuxent River, Maryland, upstream of American Shad spawning sites. Hickory Shad have been found to spawn in both the main stem and tributaries of rivers in Virginia (Klauda et al., 1991b). In the Roanoke River upstream of our study area, Harris and Hightower (2011) conducted a study of spawning habitat for Hickory Shad, and they determined that adults generally avoided spawning in areas with very low (<0.1 m/s) or no water velocity, especially when substrate sizes were small. When water velocities were low (<0.1 m/s), spawning occurred only on bedrock substrates. When water velocities were higher (≥0.1 m/s), spawning occurred on a variety of substrate types, including gravel and occasionally sand. Although we did not survey spawning habitat of Hickory Shad in the Roanoke River in 1996, both ripe and partially spent adults were collected from tributaries of the Roanoke River in the RRNWR and at Weldon. The higher flows of the Roanoke River in the spring flood the backwater tributaries and swamps; therefore, maintenance of a flow regime similar to the natural springtime flows probably is needed to ensure suitable spawning habitat for Hickory Shad in this watershed.

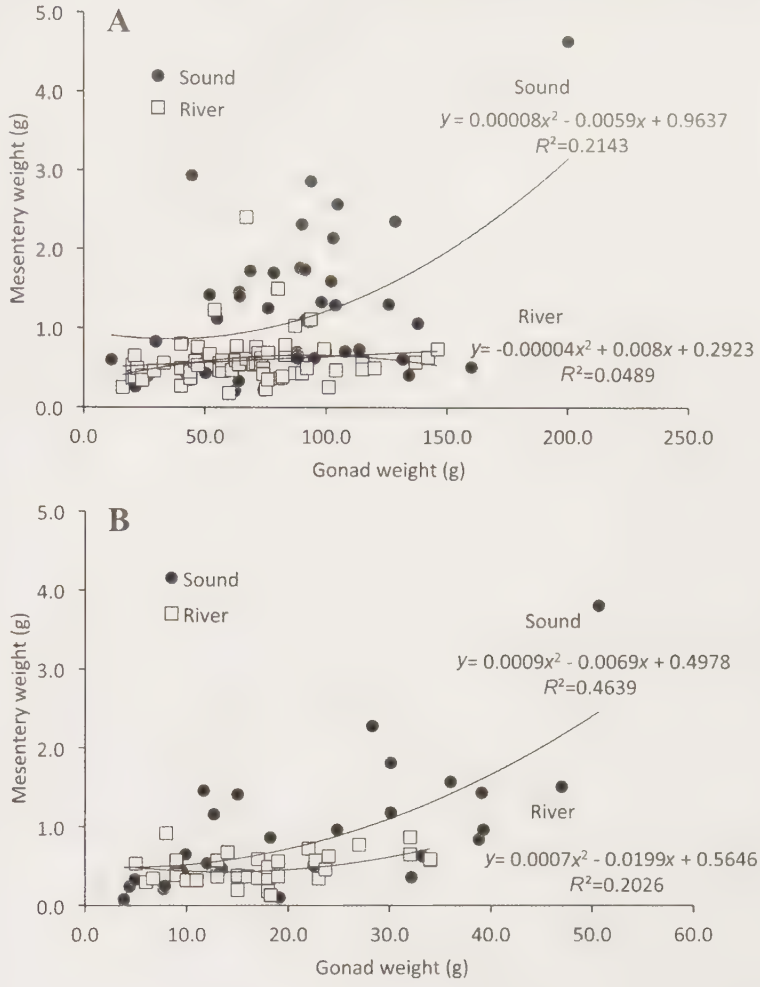

Figure 6

Relationship between mesentery fat and gonad weight, both measured in grams, of (**A**) female and (**B**) male Hickory Shad (*Alosa mediocris*) collected during February–May 1996 in Albemarle Sound and on the Roanoke River spawning grounds near Weldon, North Carolina. R^2=coefficient of multiple determination.

Why spawning runs of Hickory Shad in the 1990s far exceeded the spawning runs of American Shad in the Roanoke River–Albemarle Sound watershed remains a mystery. Historically, American Shad dominated harvests of anadromous shad in every major watershed in mid-Atlantic and South Atlantic states. Near the turn of the 20th century in 1890, North Carolina landings of American Shad totaled 2.616 million kg (5.768 million lb), increasing to 4.066 million kg (8.963 million lb) in 1897 and dropping to 2.979 million kg (6.567 million lb) in 1902 (Alexander, 1905). Hickory Shad landings were only 104,780 kg (231,000 lb) in 1897 and 310,711 kg (685,000 lb) in 1902. At the end of the 20th century (in 1996, the year of our study), commercial harvests of both species were nearly equal: 90,554 kg (199,638 lb) of American Shad and 85,244 kg (187,887 lb) of Hickory Shad (NCDMF database, http://portal.ncdenr.org/web/mf/statistics/comstat; Fig. 1). Interpretation of landings beyond 1996 becomes more difficult because the species was declared a game fish in inland waters, and harvest restrictions were subsequently put in place for the recreational fishery. How this designation of a game fish may have affected commercial harvest is unknown.

The Roanoke River fishery, once dominated by thriving commercial fisheries that targeted anadromous species American Shad, Alewife, Blueback Herring, and

Striped Bass, is now a multimillion-dollar recreational fishery best known for Striped Bass and Hickory Shad (McCargo et al.[7]). Habitat loss and fragmentation, along with overharvesting the species, are considered major factors in the reduction of alosine stocks to remnant populations in this watershed (Walsh et al., 2005; McCargo et al.[7]) and elsewhere in the North Atlantic (Limburg and Waldman, 2009). Restoration of the American Shad population in the Roanoke River has been ongoing since 1988 (Waters[24]), but adult abundance remains low despite the stocking of 43 million American Shad fry in the Roanoke River as of 2010 (Dockendorf[10]).

Populations of Hickory Shad in upper Chesapeake Bay tributaries are experiencing resurgence and are supporting an active catch-and-release recreational fishery. This resurgence also means better access to brood fish for hatchery programs, and the state of Maryland now has implemented stock restoration efforts for Hickory Shad in 3 rivers: the Patuxent, Choptank, and Nanticoke (Richardson et al.[23]). Maryland agencies hope to establish increased fishing opportunities for targeting Hickory Shad, believing that restoration of this species has the potential to occur over a shorter time frame (because of its earlier age at maturity) than the period needed for American Shad restoration (Richardson et al.[23]).

Conclusions

Our findings clearly indicate that the short lifespan of the Hickory Shad, combined with an early age to maturity and an anadromous migration pattern, means that adult individuals of the population will be subjected to recreational and commercial harvest in inland waters for 1 or 2 seasons before they are removed by exploitation or natural mortality. Our data were collected before the implementation of the 10-fish bag limit on shads. North Carolina fisheries agencies hope that a daily 10-fish limit for shads (only 1 fish can be American Shad in the Roanoke River) will protect current population size while maintaining the interest of fishermen in this lucrative fishery. The study presented here is the most recent on this species for North Carolina; data collected during creel surveys by the NCWRC have included only recorded catches but not samples for lengths, weights, or age. We recommend that new data be collected on age and growth since this regulation went into effect to determine whether incidences of repeat spawning events have increased in this population. This growing population has a sex ratio slightly dominated by females both in the prespawning staging area in Albemarle Sound in January and on the spawning grounds in the Roanoke River. Continued research on the poorly understood life history of this species will increase our understanding and, perhaps, provide insight on its success in relative abundance compared with that of American Shad.

[24]Waters, C. T. 2000. Summary of activities in 1998 and 1999 for restoring American Shad to Roanoke River. [Available from North Carolina Wildlife Resources Commission, 1751 Varsity Dr., Raleigh, NC 27606.]

Acknowledgments

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Errata

Fishery Bulletin 112:49–70.

Munyandorero, Joseph
In search of climate effects on Atlantic Croaker (*Micropogonias undulatus*) stock off the U.S. Atlantic coast with Bayesian state-space biomass dynamic models

Corrections:

On page 56, Equation 6 is missing an equal sign in the calculation of the deviance statistic D. The equation should read as follows:

$$D(\Theta) = -2\log L(\Theta) = -2\log\left[P(O \mid \Theta)\right]$$

On page 70, the age symbol in Equation A2 should be a, instead of α (alpha). Equation A2 should read as follows:

$$F_a = \beta\left\{L_\infty\left[1-\exp(-K(a-a_0))\right]\right\}^\gamma$$

National Marine Fisheries Service Best Paper Awards for 2013

The award for best publication of the year is given to authors who are employees of the National Marine Fisheries Service and whose article is judged to be the most noteworthy of those published in *Fishery Bulletin* and *Marine Fisheries Review*. The selections were made by scientists at all NOAA Fisheries Science Centers and thus represent well-deserved recognition by peers. Authors from the National Marine Fisheries Service are noted in bold font.

The winners for *Fishery Bulletin*

Rose, Craig S., Carwyn F. Hammond, Allan W. Stoner, J. Eric Munk, and John R. Gauvin
Quantification and reduction of unobserved mortality rates for snow, southern Tanner, and red king crabs (*Chionoecetes opilio, C. bairdi, and Paralithodes camtschaticus*) after encounters with trawls on the seafloor
Fish. Bull. 111:42–53.

This clearly written paper presents an excellent study of an important topic for ecosystem-based fisheries management. The problem of unobserved mortality of bycatch is a consequential yet unaccounted for aspect of numerous fishery operations and is of worldwide concern. The paper efficiently describes a well-thought-out and well-executed approach to quantification of unobserved and unintended mortalities of commercially valuable crab species that encounter bottom trawls targeting ground-fish in the Bering Sea. Care was taken in the design of the experiments and in the thoroughness of the research and this paper provides a practical, low-cost, and innovative method for reducing crab bycatch mortality rates while maintaining catch levels for target fish species. Moreover, the authors went beyond quantification of unobserved crab mortalities and incorporated the design and testing of modified trawl gear, which—if adopted by commercial fishing fleets—could mitigate bycatch mortalities. This kind of research can be tedious, but it is only through just such studies that a real understanding of the effects of trawling and the extent of unobserved mortality rates can be obtained. This work addresses a breadth of questions and provides practical management insights (based on a well-defined model) that could be expanded for the study and management of other species.

The winner for *Marine Fisheries Review*

Castro, Jose
Historical knowledge of sharks: ancient science, earliest American encounters, and American science
Mar. Fish. Rev. 74(4):1–26.

This impressive, particularly well-written and researched compendium of shark information demonstrates how sharks have interacted with humans over time and how our understanding and study of these often misunderstood creatures have progressed since antiquity. This paper is of wide interest and utility to those who study the biology of sharks and their use by humans. It is the result of a monumental undertaking that required numerous years of research to amass the knowledge and material that is presented. This type of effort is time consuming and sometimes underappreciated. The paper highlights the value of older documents that are not available to any but the most scholarly of scientists with avid interest in fisheries history. For example, rare pictures and engravings of sharks show progressively more sophisticated and detailed depictions through several centuries up to the present time. This paper will keep alive such past works that are difficult to find and allow them to still contribute to current scholarly works and research efforts. The detailed explanation of how sharks have been utilized over time and how fisheries operated in the past passes on information that is available to few. Dr. Castro, for example, has one of the only surviving documents from the Ocean Leather Company. His discussion of the history of this company and how it is intertwined with past U.S. fisheries and research will enlighten even the most seasoned shark researcher. This article is truly an interesting and detailed work by one of the world's foremost experts on sharks.

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Fish and fishes For papers on taxonomy and biodiversity, the plural of *fish* is *fishes,* by convention. In all other instances, the plural is *fish.*

Examples: The fishes of Puget Sound [biodiversity is indicated];
The number of fish caught that season [no emphasis on biodiversity];
The fish were caught in trawl nets [no emphasis on biodiversity].

The same logic applies to the use of the words *crab* and *crabs, squid* and *squids,* etc.

Sex For the meaning of male and female, use the word *sex*, not *gender.*

Participles As adjectives, participles must modify a specific noun or pronoun and make sense with that noun or pronoun.

Incorrect: *Using the recruitment model, estimates of age-1 recruitment were determined.* [Estimates did not use the recruitment model.]

Correct: *Using the recruitment model, we determined age-1 estimates of recruitment.* [The participle now modifies the word *we,* those who were using the model.]

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Tables are often overused in scientific papers; it is seldom necessary or even desirable to present all the data associated with a study. Tables should not be excessive in size and must be cited in numerical order in the text. Headings should be short but ample enough to allow the table to be intelligible on its own. All unusual symbols must be explained in the table legend. Other incidental comments may be footnoted with italic numeral footnote markers. Use asterisks only to indicate significance in statistical data. Do not type table legends on a separate page; place them above the table data. *Do not submit tables in photo mode.*

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